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Availability of soil water to plants

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AVAILABILITY OF SOIL WATER TO PLANTS

by

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INTRODUCTION

Potential transpiration has been defined by Penman (1956) as the amount of water transpired in unit time by a short green crop, completely shading the ground, of uniform height and never short of water. Penman makes two broad generalizations concerning potential transpiration:

1. For complete crop covers of different plants having about the same color, i.e. the same reflection coefficient, the potential transpiration rate is the same, irrespective of plant or soil type.
2. This potential transpiration rate is determined by prevailing weather.

Most of the research in the evapotranspiration problem in recent years has been directed towards examining the validity of these generalizations, and in general, has succeeded in doing so. Little attention has been given to the question: What happens when soil water becomes a limiting factor, i.e. at what soil moisture content does the actual transpiration rate fall below the potential rate and can this be predicted for any given soil-plant-weather combination?

Water movement in the transpiration stream involves three phases, namely, water movement in the soil to the root, water movement in the plant to the leaf, and vapor movement from the leaf to the air. Under the conditions of potential transpiration, the crop is never short of water. This ensures

that resistance to water movement in the soil and in the plant is small. Then, the weather conditions determining vapor movement from the leaf to the air are the dominant factors in determining transpiration rate, and Penman's generalizations concerning potential transpiration are sufficiently correct for practical applications. As soil moisture supply decreases, the resistances to water movement in the soil and in the plant increase considerably and the generalizations for potential transpiration no longer apply.

The present dissertation represents an attempt to combine these three phases of transpiration into a dynamic theory of water movement in the transpiration stream. An analogy with heat flow will be used to describe the flow of water in transpiration and to predict, at least qualitatively, actual transpiration rates under different soil moisture regimes and different weather conditions. Comparison of the theory with experimental observations will be made.

REVIEW OF LITERATURE

Water Movement in the Soil

Buckingham (1907) suggested the term "capillary potential" to express the value which measures the attraction of the soil for water at any given point. He visualized that the flow of water through soil occurs in response to a difference in capillary potential between two points in the soil which are at different moisture contents, in the same manner as heat flows through a bar between two points which are at different temperatures. The capillary potential would be defined as the work required to move a unit mass of water, against capillary forces in a column of soil, from a free-water surface to the particular point in the soil. Since capillary forces are negative because of the greater inward attraction of the water molecules at the air-water interface, the capillary potential would be negative in sign.

Childs and Collis George (1948) pointed out that capillary forces are not the only ones acting upon the water in the soil. There are at least four components of the total force involved:

1. The gravitational potential.
2. The hydrostatic pressure potential due to the different air-water interfaces in the system. This is the pressure potential arising from the capillary

forces discussed in the preceding paragraph.

3. The osmotic pressure potential arising from the presence of soluble salts or differences in the dissociation of adsorbed ions on the surface of colloidal particles.
4. The adhesive potential due to the attraction of oriented dipole water molecules on the surface of the particles.

The total moisture potential Φ arises from the combined effects of these four forces. In modern soil physics the last three forces are grouped together as the capillary potential. Since all three act to promote pressure deficiencies, the capillary potential has units of negative pressure. Commonly the negative sign is ignored and one refers to positive units of soil suction. The soil suction is then the work done against field forces in moving a unit mass of water from a free water surface to the point in question. The gravitational potential is usually denoted by the symbol $\emptyset$ and the soil suction by the symbol ψ. The units of moisture potential are commonly centimeters of water or bars.

The flow of water in a saturated porous medium is described by Darcy's law in the form

$$v = - K \nabla \Phi \qquad (1)$$

where v is the volume of water crossing unit cross-sectional

area perpendicular to the direction of flow in unit time, the common units being cm. sec.$^{-1}$, K is the hydraulic conductivity or the volume of water which will flow in unit time across a unit cross-sectional area of soil perpendicular to the direction of flow, when the value of Φ changes at the rate of one unit per unit distance, the common units being those of velocity cm. sec.$^{-1}$, and $\nabla\Phi$ is the gradient of the moisture potential. It will be noticed that this form of Darcy's law is similar to the generalized forms of Fourier's law of heat flow, Ohm's law of electricity and Fick's law of diffusion.

Darcy's law applies to the flow of water in a saturated porous medium. Since we are commonly dealing with unsaturated flow in the soil, it is desirable to be able to describe unsaturated conditions also. Richards (1931) extended Darcy's law to unsaturated flow as also did Childs and Collis George (1948); on the assumption that K is a function of the moisture content, they found that Darcy's law was still applicable.

By combining the equation of continuity and the general form of Darcy's law in Equation 1, a general partial differential equation describing soil water flow in the unsaturated state can be developed (Klute, 1952). For one dimensional flow in the horizontal, x, direction, the equation becomes

$$\frac{\partial \theta}{\partial t} = \frac{\partial}{\partial x} K\left[\frac{\partial \Phi}{\partial x}\right] = \frac{\partial}{\partial x} K\left(\frac{\partial \psi}{\partial x} + \frac{\partial \phi}{\partial x}\right)$$

$$= \frac{\partial}{\partial x}\left[\left(K \frac{\partial \psi}{\partial \theta}\right) \frac{\partial \theta}{\partial x}\right] \qquad (2)$$

where θ denotes the volume fraction of water in the soil, t denotes time and K, Φ, ψ and ϕ are as previously defined. If θ and ψ are considered to be related by a single-valued function, then Equation 2 becomes

$$\frac{\partial \theta}{\partial t} = \nabla \cdot (D \nabla \theta) \qquad (3)$$

In Equation 3, D is the diffusivity, defined by the relation

$$D = K \frac{\partial \psi}{\partial \theta}$$

where both K and $\partial \psi / \partial \theta$ are considered functions of the moisture content of the medium, θ. Thus, if K and ψ are known as functions of θ, D can be calculated and expressed by a curve as a function of θ. One can visualize diffusivity as the rate of water movement per unit gradient of soil moisture content. It has units of $cm.^2$ $sec.^{-1}$. When dealing with unsaturated flow, it is conventional to refer to K as the capillary conductivity to distinguish it from the constant hydraulic conductivity for a saturated medium. As saturation is approached, capillary conductivity approaches the hydraulic conductivity. The reciprocal of the term $\partial \psi / \partial \theta$ is analogous to the specific heat in the theory of heat flow. Klute (1952) refers to it as the "specific moisture capacity". Experi-

mental methods are available for determining both ψ (Nielsen, 1958) and K (Nielsen, 1958 and Gardner, 1956) as functions of θ in the unsaturated state.

For radial flow in a two-dimensional radially-symmetrical horizontal region around a point in the soil, such as the center of a vertical root, Equation 3 becomes

$$\frac{\partial \theta}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left(rD \frac{\partial \theta}{\partial r} \right) \qquad (4)$$

where r denotes radial distance from the point in question. Equation 4 has been used to describe the movement of water in the soil in the course of transpiration by Philip (1957) and Gardner (1960) and will be referred to in a later section.

Water Movement in the Plant

This discussion will be restricted to the case of passive absorption of water by the plant. The classical concept of the water relations of plant cells is well known and will be discussed only briefly here. Detailed discussion has been given by Crafts, Currier and Stocking (1949), Richards and Wadleigh (1952), and Slatyer (1960).

The diffusion pressure deficit, DPD, of a cell is equal to the difference between the osmotic pressure of the cell contents and the turgor pressure of the cell, which is the hydrostatic pressure with which the cell contents press against the cell wall. DPD measures the net tendency of water

to enter the cell. As water moves from the cell, say in the course of transpiration, the osmotic pressure of the cell contents increases slightly and the turgor pressure decreases. Thus, DPD, which is the difference between osmotic pressure and turgor pressure, increases. DPD approaches its maximum value as wilting is approached since the turgor pressure of the cell is then approaching a value of zero. DPD has its lowest value, zero, when the cell is fully turgid and the turgor pressure balances the osmotic pressure. The units of DPD are generally those of pressure, centimeters of water or bars.

Continuity of thought with reference to the movement of water from the soil to the plant will be aided by bearing in mind that soil moisture suction is identical in concept and dimensions with the DPD of the water in the soil. Just as movement of water in the soil is assumed to result from a gradient in soil suction, so also is movement of water from soil to plant assumed to result from a gradient in DPD from the soil to the root. Experimental data supporting this latter assumption have been provided by Hayward and Spurr (1944). Working with corn roots in solutions of different osmotic pressure, which, for soil, would mean a soil at different values of soil suction, they found a negative linear relationship between rate of water entry into the roots and increasing values of osmotic pressure in the solution. Move-

ment of water within the plant is also assumed to result from a gradient in DPD from tissue to tissue, normally from base to apex. Richards and Wadleigh (1952) cite many experimental observations of this phenomenon.

The DPD gradient within the plant is assumed to be proportional to the transpiration rate (Van den Honert, 1948). If the permeability of the plant were to remain constant, a given transpiration rate would require a specific gradient of DPD between the top and the root of the plant. It has been pointed out in a previous paragraph that there is a maximum DPD which can be developed in the tissues of a plant. This is the DPD just prior to the complete loss of turgor in the cells, and it approaches the maximum osmotic pressure developed in the cell contents. Hence, the statement that a given transpiration rate would require a specific DPD gradient between the top and the root of the plant implies that there is an upper limit to the transpiration rate from a plant, although, to date, the author has seen no experimental observations of such a phenomenon reported in the literature.

Available Water, Field Capacity and the Wilting Point

Agronomists frequently use the term "available water" to denote the fraction of the soil water which is available to plants for transpiration and growth. Available water is commonly considered to be that water held in the soil between

field capacity and the wilting point. Field capacity represents an upper limit to the water which a soil can retain against drainage. It is defined as the moisture content of a soil, determined in the field some 72 hours after a heavy rain or irrigation, when the excess gravitational water has drained away and when the rate of downward movement of water has materially decreased. Thus, field capacity represents the upper limit to the water content of a soil in the unsaturated condition. For most soils, field capacity corresponds to a soil suction of 0.03 to 0.2 bar (Richards and Wadleigh, 1952).

As defined by Baver (1956), the wilting point denotes that soil moisture content at which the soil cannot supply water to the plant at a sufficient rate to maintain turgor. In the light of the foregoing discussion of the water relationships within the plant, the wilting point, then, represents the soil moisture content at which the turgor pressure in the plant tissues is reduced to zero and the DPD in the tissues has attained its maximum value.

The concept of the permanent wilting point was first introduced by Briggs and Shantz (1912). They grew plants in pots in which evaporation from the soil surface was prevented. The moisture content of the soil was determined when the plants permanently wilted, i.e. when they would not recover turgor when placed in a saturated atmosphere. This

same procedure, using sunflowers as the test plant, is still frequently used to determine the permanent wilting point of a soil. Briggs and Shantz contended that the permanent wilting point is a constant for a given soil. Veihmeyer and Hendrickson (1948) also asserted that the permanent wilting point is a constant characteristic of the soil, irrespective of environmental conditions under which plants wilt in the field. Empirically, it is found that the moisture retained in a sample of soil that has been wetted and brought to hydraulic equilibrium with a porous membrane at 15 bars pressure corresponds closely to the permanent wilting point for most soils (Baver, 1956). Because of the ease of determination and the ability to standardize conditions, many agronomists now use the 15 bar percentage for the permanent wilting point.

Although the permanent wilting point may be an approximate soil constant, it is not an index of soil water availability under field conditions. By Baver's definition, the wilting point is a dynamic rather than a static concept. It is determined by the rate at which water is supplied to the plant. Obviously then, the wilting point must depend on the transpiration rate, since the transpiration rate determines the DPD within the plant tissues and thus, the rate at which water must be supplied to the plant in order to maintain turgor. The wilting point must also depend on the average

soil suction since we have seen that the rate of water movement in the soil is proportional to the gradient in soil suction. Again, it must depend on the capillary conductivity of the soil which also influences the rate of water movement in the soil. The wilting point will be examined in relation to these variables in a later section.

Vapor Movement from Leaf to Air

At the leaf, water is being evaporated into the air. From the interface between the mesophyll cells of the leaf and the intercellular spaces where evaporation occurs, water movement is a diffusion of water vapor up through the stomata to the circulating air. As outlined by Van den Honert (1948), the potential gradient in this phase corresponds to the difference in water-vapor pressure and is usually expressed as a difference in relative humidity or vapor pressure deficit. However, for comparison, this potential gradient may also be expressed in bars of osmotic pressure or DPD, (e.g., Philip, 1957). Even at high relative humidities the DPD values of the atmospheric air are considerable, quite often of the order of 1,000 bars, as illustrated by Shull (1939). The rate of water movement in the gaseous phase is determined not only by a DPD gradient but also by the resistance to water-vapor diffusion through the saturated air layer surrounding the mesophyll cells and extending up through

the stomata to the free air.

In a moist soil, the DPD of the root environment, i.e. the soil suction, is on the order of 0.2 bar. As put by Gradmann (1928), if one assumes a relative humidity of 47 per cent at an air temperature of 70°F., then the plant is inserted as a water conducting medium between two media with DPD values of 0.2 and 1,000 bars respectively. A continuous current of water passes inside the plant from lower to higher DPD values, successively through root cells, xylem, mesophyll and the gaseous part (including the stomata). The DPD value in the mesophyll cells of the leaf rarely exceeds 50 bars. Thus, the DPD gradient from leaf cell to air is 19 times as great as the total resistance to water movement within the plant from soil to leaf.

Van den Honert (1948) supported this conclusion and calculated that the vapor shell, or layer of saturated air adherent to the leaf, was about 0.4 mm. to 10 mm. thick, depending on the strength of the wind blowing over the leaf, and that the resistance to the diffusion of water vapor through such a layer was of the order of magnitude suggested by Gradmann. Van den Honert concluded that, judging from the gradient of DPD values through the plant into the air, by far the greatest resistance in the total water transport is situated in the gaseous part, and this great resistance is a physical reality. The resistance to water movement imposed

by the necessity for vapor diffusion through this stationary saturated air film over the surface of the leaves makes it possible for plants to tolerate conditions where the desiccating power of the air is relatively enormous.

Attempts have been made to determine analytically the resistance to water vapor diffusion from the surface of the leaf mesophyll cells to the free air (Penman and Schofield, 1951; Bange, 1953; Penman, 1956; and de Wit, 1958). An example of the use of this approach is afforded by the equation developed by de Wit (1958) for the transpiration of a single leaf:

$$T = \frac{\Delta}{(\Delta + s\gamma)V} R_{n_l} + 2 h_w(t_a - t_d)$$

where T is the transpiration rate per unit area of leaf in $g.cm.^{-2}min.^{-1}$, Δ is the slope of the saturation vapor pressure vs. temperature curves at the air temperature in units of mm. Hg $°C^{-1}$, γ is the psychrometric constant in units of mm. Hg $°C^{-1}$, s is a factor representing the resistance to water vapor diffusion and is equal to $(L_a + L_s)/L_a$ in which L_a and L_s are diffusion lengths in air and in the stomata, respectively, in cm. (the diffusion length is the thickness of the gaseous layer through which the water vapor is diffusing; for the stomata, L_s is a function of the shape, aperture and number of the stomata), V is the latent heat of vaporization in units of $cal.g.^{-1}$, R_{n_l} is the net radiation

gain per unit area of a single leaf in cal. $cm.^{-2}$ $min.^{-1}$, h_w is the heat transfer coefficient, which is the same for a wet filter paper of the same dimensions in units of cal. $cm.^{-2}$ $min.^{-1}$ $°C^{-1}$, t_a is the air temperature in °C, and t_d is the dew point temperature of the air in °C. Unfortunately, considerable difficulty is experienced in obtaining reasonable estimates of s and h_w and to date it has been found more convenient to estimate transpiration rate by other methods.

Measurement of Transpiration

Evaporation from free-water surfaces, from the surfaces of porous media well supplied with water such as a moist soil, and from vegetative surfaces (transpiration), has been extensively studied. The most important factors determining evaporation rate are:

1. the amount of energy available for vaporization of water,
2. the existence of a transport mechanism to move the water vapor away from the air layers close to the evaporating surface into the atmosphere,
3. the supply of water at the evaporating surface,
4. for plants, the regulation of the diffusion of water vapor through the stomata by stomatal closure.

Measurements of evaporation from a plant cover can be

made either by measuring the water loss from the soil or, since evaporation depends on weather conditions, by micrometeorological methods. Measurements of water loss from the soil include direct measurements such as gravimetric sampling and indirect measurements such as those made by use of tensiometers, electrical conductivity units, thermal conductivity measurements or by measurement of neutron scattering. A review of direct and indirect methods for the field determination of soil moisture has been given by Taylor (1955). The errors involved in measurement of soil moisture by neutron scattering have been analysed by Stone et al. (1960).

Studies on the use of micrometeorological methods for measuring evaporation from plant covers are numerous. The methods used may be grouped into two main classes, energy balance methods and aerodynamic methods. Energy balance methods are based on the fact that evaporation is a change of state, demanding a supply of energy as heat of vaporization. The primary source of this energy is solar radiation. When incoming solar radiation reaches a crop or soil surface, some of it is reflected, some is absorbed and some is re-radiated to the atmosphere. The energy that is absorbed and not re-radiated is known as net radiation. Thus net radiation R_n is given by the expression

$$R_n = R_s(1 - r) - R_b$$

where R_s is the incoming solar radiation, r is the reflection coefficient (albedo) of the absorbing surface, and R_b is the re-radiated energy from the surface to the atmosphere.

The net radiation may then be partitioned into evaporation of water E, energy used in storage (heating the crop and the soil) S, sensible heat transfer to the air A, and energy used in photosynthesis P. Thus,

$$R_n = E + S + A + P$$

Net radiation can be measured rather simply with appropriate instruments, e.g., the net radiometers described by Gier and Dunkle (1951) and Fritschen (1960). The problem is to measure the components S, A and P so that evaporation is left as the only unknown. A detailed discussion of the energy balance approach to evapotranspiration from crops has been given by Tanner (1960).

Aerodynamic methods of measurement attempt to measure the turbulent transport of water vapor away from the crop surface. The necessary mathematical argument is given in many texts on meteorology, e.g., Sutton (1953). Typical of the evaporation equations commonly used for estimating transpiration is that developed by Thornthwaite and Holzman (1942) and by Rider (1954), viz.,

$$E = \frac{\rho k^2 (q_1 - q_2)(u_2 - u_1)}{\left[\ell n\{(z_2 - d)/(z_1 - d)\}\right]^2}$$

where E is the evaporation rate, ρ is the density of air, $k = 0.41$ is von Karman's constant, q_1 and q_2 are the concentrations of water vapor at heights z_1 and z_2 above the ground surface, u_1 and u_2 are the horizontal wind velocities at these same heights, and d is a parameter characteristic of the crop which can be estimated from wind profile measurements. The successful application of aerodynamic methods of measurement requires rather precise measurement of the vertical profiles of wind velocity, vapor pressure and temperature. Penman (1948, 1956) and Makkink (1957) have combined the energy balance method and the aerodynamic method so that evaporation can be estimated from readily available meteorological data.

Discussions of the use of these various methods for estimating evaporation have been presented by Penman (1956), de Wit (1958), Scholte Ubing (1959) and Tanner (1960). Suffice it to say here that transpiration rates can be estimated from meteorological measurements with quite reasonable accuracy when soil moisture supply is not limiting. For a well developed crop cover not short of water, it has been found that transpiration rate is closely related to evaporation from a free water surface. The problem of predicting transpiration rate when the rate of water supply to the plant is limited by low soil moisture is more complicated. As well as meteorological factors, both soil and plant characteristics are involved.

The Flow Equation Applied to Transpiration

In the previous pages, it has been shown how the water in the soil, the plant and the atmosphere forms a continuum on an energy basis. In the course of transpiration, water moves through the soil to the plant roots and through the plant to the mesophyll cells of the leaf along energy gradients moving from regions of higher potential (lower suction or DPD) to regions of lower potential (higher suction or DPD). At the leaf, water is being evaporated into the atmosphere, the necessary energy for vaporization being supplied mainly by solar radiation. The evaporated water is removed from the leaf surface by turbulence and convection and by vapor pressure gradients.

Evaporation of water from the leaf mesophyll cells increases the DPD of water in the leaf and a gradient of DPD from leaf to root is thus established. If the DPD in the root is higher than the suction in the soil water adjacent to the root, water will move from the soil into the root and then to the leaves. As the soil around the root dries, the suction of the soil water increases and thus, if a constant transpiration rate is to be maintained to meet the evaporative demand of the atmosphere, the DPD in the root required to remove water from the soil, must also increase. As long as the DPD in the root is higher than in the surrounding soil, water will move from the soil to the plant and transpiration

can proceed. As the suction of the soil water around the root increases, water moves toward the root from the soil at a small distance away from the root (where the soil suction is lower) in response to the suction gradient established in the soil water.

Philip (1957) has given a biophysical model of transpiration which depicts graphically the energy status at various points along the transpiration path. As a summary of the concepts discussed thus far, a simplified version of this model is presented in Figure 1.

In Figure 1, curve 1 represents the situation when the soil moisture content is high; the water in the soil is held at low suction and the capillary conductivity is high. As a result, the DPD in the root is low. A difference in DPD between the roct and the mesophyll cells of the leaf is necessary to produce the flow of water between these regions. This difference is proportional to the transpiration rate. The difference is small enough that, at this stage, the DPD in the mesophyll cells remains below the critical level at which turgor is lost. This critical value of DPD, which is the maximum value of DPD that can be developed, is designated as DPD_w and in this case is shown arbitrarily as 25 bars.

Curve 2 represents the same plant transpiring under the same meteorological conditions but with the soil moisture somewhat less. The soil suction is higher and the capillary

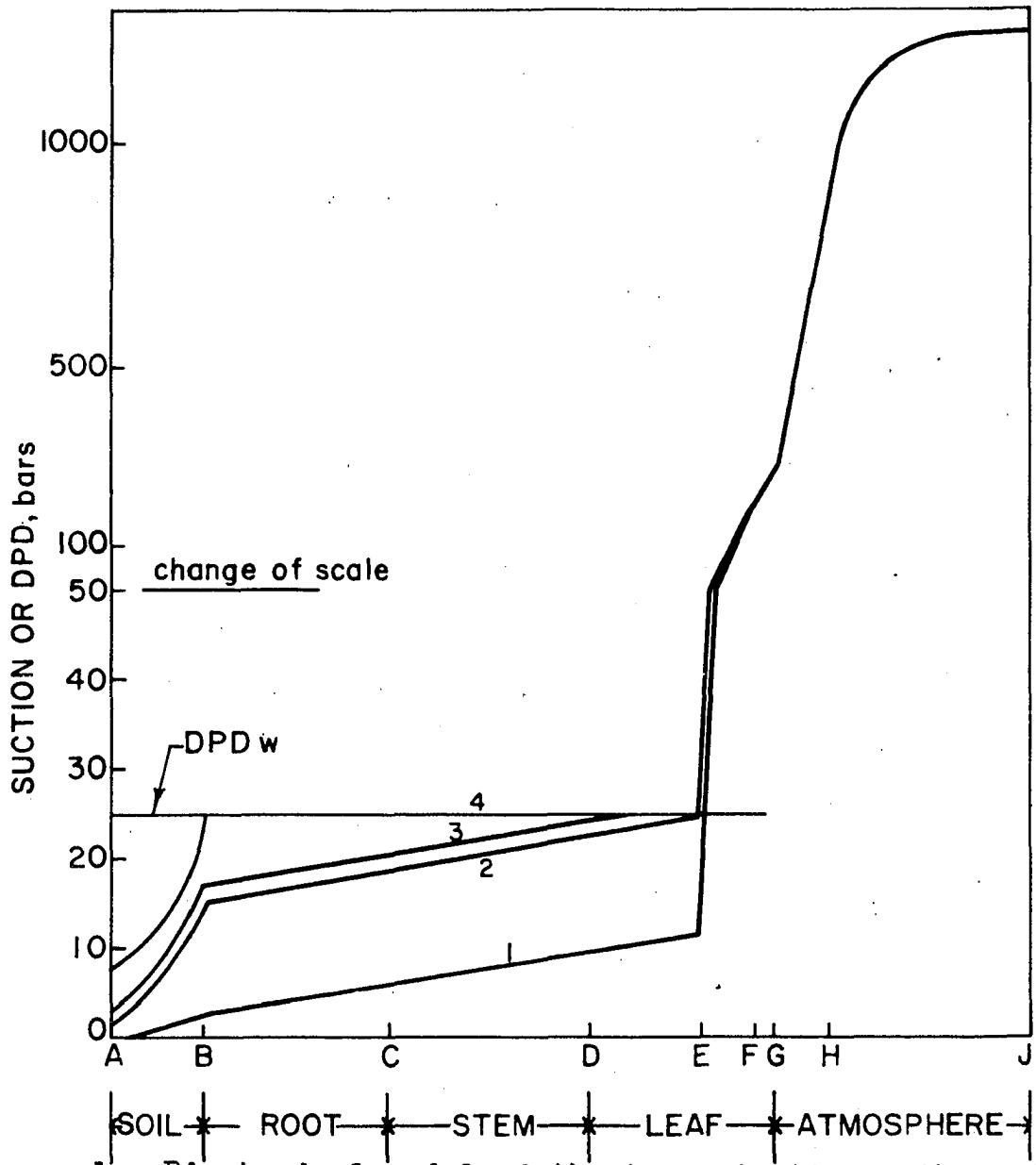


Figure 1. Biophysical model of the transpiration path depicting the energy status at various points along the path (after Philip, 1957). Points on the path: A. Soil (at the boundary of the region of influence of the root); B. Surface of the root; CD. Stem; D. Leaf veins; E. Mesophyll cells; EF. Intercellular space and substomatal cavity; FG. Stomatal pore; GH. Stationary air layer adhering to leaf; HJ. Turbulent boundary layer and free atmosphere. See text for explanation of curves 1, 2, 3, and 4

conductivity is less so that the DPD in the root has increased appreciably. In order to maintain the same transpiration rate as represented by curve 1, there must be the same difference in DPD between leaf and root. Thus, the DPD in the mesophyll cells must increase. At this stage, it is approaching the maximum value of 25 bars.

Curve 3 represents the situation when the soil moisture has decreased further. Again soil suction has increased and capillary conductivity has decreased so that the DPD in the root has increased still further. Now, the DPD in the leaves of the upper part of the plant cannot rise any higher than DPD_w and turgor in these leaves is lost. The gradient in DPD from leaf to root is less than that needed to maintain the potential transpiration rate so that actual transpiration rate has decreased.

Curve 4 represents the situation with soil moisture still less. Soil suction is higher, capillary conductivity is lower and the DPD in the root has risen to DPD_w. Now, the DPD in all parts of the plant has risen to DPD_w and the whole plant loses turgor and wilts. Transpiration rate is now zero.

This problem can be analyzed mathematically by making use of the equation describing water movement in unsaturated soil, Equation 4. This approach has been followed by Philip (1957) and more recently by Gardner (1960). In order to

apply the flow equation, it is necessary to make some assumptions about root geometry. The problem is simplified by assuming cylindrical geometry. Gardner takes the root to be an infinitely long cylinder of uniform radius and water-absorbing properties, and assumes that water moves only in the radial direction. Gardner points out that because of the complex structure and geometry of plant roots, this is only an approximation. In some regions the geometry will be more nearly spherical and in others perhaps more nearly linear. The exact geometry is not critical, however, and does not affect the conclusions materially.

Philip's approach is somewhat more elegant. He replaces the rather irregular absorbing surface of the root occurring in nature--typically roots with their accompanying root hairs protruding, like spokes, normal to their surface--by a cylindrical surface with area equal to the absorbing surface and of length equal to the total length of the roots. To a good approximation, says Philip, the absorbing area is equal to the area of the root hairs. Then the region of influence of the simplified root may be taken as a cylinder of soil of such radius that the volume of soil per unit of absorbing surface equals that occurring in nature.

The two approaches give essentially similar results. For convenience, Gardner's somewhat simplified approach will be followed here.

The flow equation is:

$$\frac{\partial \theta}{\partial t} = \frac{1}{r} \frac{\partial}{\partial r} \left(rD \frac{\partial \theta}{\partial r} \right) \qquad (4)$$

The initial water content will be assumed to be uniform throughout the root zone with some value θ_o corresponding to a soil suction ψ_o. We examine the suction required at the boundary between the plant root and the soil in order to maintain a constant rate of water movement to the root. The initial and boundary conditions are:

$$\begin{aligned} &\theta = \theta_o , \quad \psi = \psi_o , \quad t = 0 \\ &2\pi aK\left(\frac{d\psi}{dr}\right) = 2\pi aD\left(\frac{d\theta}{dr}\right) = q , \quad r = a \end{aligned} \qquad (5)$$

where a is the radius of the root in cm., K is the capillary conductivity of the soil in cm. $sec.^{-1}$ or cm. day^{-1}, D is the diffusivity for soil water flow in $cm.^2$ $sec.^{-1}$ or $cm.^2$ day^{-1}, and q is the rate of water uptake by the root, expressed as volume of water per unit length of root per unit time, in units of $cm.^2$ $sec.^{-1}$ or $cm.^2$ day^{-1}. q is directly proportional to the transpiration rate.

Since K and D vary markedly with soil water content, the flow equation is difficult to solve exactly. However, if typical constant values are assigned to K and D, an approximate solution which retains most of the significant features of the exact solution is fairly readily obtained. The justification for assuming constant K and D will be examined

later in this section.

The solution of Equation 4 subject to the Conditions 5 is obtained by analogy to the flow of heat into an infinitely long cylinder of radius a. The equation of heat flow for radial flow is given by Carslaw and Jaeger (1959, p. 188) as

$$\frac{\partial v}{\partial t} = D\left(\frac{\partial^2 v}{\partial r^2} + \frac{1}{r}\frac{\partial v}{\partial r}\right) \qquad (6)$$

where v denotes temperature, D is the diffusivity for heat flow, and t and r again denote time and radial distance, respectively. For D constant, Equation 4 may be written in the same form as the above equation. The solution to Equation 6 for zero initial temperature and a constant flux of Q heat units per unit time per unit area at r = a, and for large values of time is given by Carslaw and Jaeger (1959, p. 339) as

$$v = \frac{Qa}{2K}\left(\ell n \frac{4Dt}{r^2} - \gamma\right) \qquad (7)$$

where v, Q, a, D, t and r have the same meaning as above, K is the thermal conductivity of the medium and $\gamma = 0.57722...$ is Euler's constant. For a constant flux of q units of heat per unit time per unit length of cylinder ($Q = q/2\pi a$), Equation 7 becomes

$$v = \frac{q}{4\pi K}\left(\ell n \frac{4Dt}{r^2} - \gamma\right)$$

For soil water flow, the solution can be expressed in terms of soil water content θ or soil suction ψ. For our purposes,

we will express the solution in terms of ψ, thus

$$\psi - \psi_o = \Delta\psi = \frac{q}{4\pi K}\left(\ell n \frac{4Dt}{r^2} - \gamma\right)$$

We are interested in the value of ψ at the surface of the root, i.e. at r = a. Thus, we write

$$\psi - \psi_o = \quad = \frac{q}{4\pi K}\left(\ell n \frac{4Dt}{a^2} - \gamma\right) \qquad (8)$$

where ψ is the value of the soil suction at r = a, and ψ_o is the initial soil suction or the value of ψ at the boundary of the region of influence of the root.

In obtaining the solution of the flow equation, it has been assumed that there is a constant flux of water to the roots, which implies a constant transpiration rate. In any real case, uptake is more nearly a sinusoidal function of time, with the suction at the plant root fluctuating about a mean value which increases to a maximum during the day, decreases at night and then increases during the course of the following day. We will deal with this mean suction, using average daily uptake rates rather than instantaneous values.

An inspection of Equation 8 shows that the increase of suction at the plant root is proportional to the rate of water uptake and is inversely proportional to capillary conductivity. These two factors, in addition to the average soil suction, are the most important factors affecting the suction at the plant root. Because diffusivity, time and

radius of the root occur in the logarithmic term in the equation, $\Delta\psi$ is much less sensitive to these three factors. Gardner (1960) points out that a ten thousand-fold increase in D would cause only about a nine-fold variation in $\Delta\psi$. Since we are concerned with a rather narrow range of soil water content, the assumption of an average, constant value of D will not be a serious restriction. Likewise, calculations of Carslaw and Jaeger (1959, p. 338) show that a ten-fold increase in root radius will produce less than a two-fold decrease in $\Delta\psi$. Thus, root radius can vary within fairly wide limits without affecting the conclusions about $\Delta\psi$ appreciably.

The assumption of constant K does lead to some error in conclusions about $\Delta\psi$, particularly at the lower values of soil suction where there is a comparatively large change in the value of K for a small change in ψ or θ. At higher suctions the errors are not so great. Gardner (1960) points out that the steady-state solution for flow in a hollow cylinder is

$$\psi - \psi_o = \Delta\psi = \frac{q}{4\pi k} \ell n \left(\frac{b^2}{a^2}\right) \qquad (9)$$

where ψ_o is now the suction at the outer radius of the cylinder r = b, and ψ is the suction at the inner radius r = a. If we were to take $b = 2\sqrt{Dt}$, Equation 8 would become identical with Equation 9 except for the constant term γ.

r_o is relatively small so that the distribution of suction in the transient case as given by Equation 8 is not very different from that in the steady-state case, with all the water coming from a distance $b = 2\sqrt{Dt}$. The distance b depends on root density and represents one-half the average distance between neighboring roots. Again, since b enters in the logarithmic term its exact value is not critical. The transient case can be approximated, therefore, by a series of steady-state solutions. The solution at any time for the transient case can be approximated by a steady-state solution corresponding to the appropriate value of ψ_o and rate of water uptake q and using the values of D and K corresponding to ψ_o. In this way, variation of K with suction (or water content) can be taken into account. This approach has been used in later sections of this thesis to follow the course of transpiration as average soil suction increases, and to investigate variation of the wilting point in relation to variation in transpiration rate.

Experimental Observations of Transpiration in Relation to Soil Moisture Content

The work of Veihmeyer and Hendrickson (1955) would indicate that soil water is readily available for transpiration as soil moisture content declines from field capacity to the 15-bar percentage. They cite many experiments in which transpiration rate did not appear to decrease until the soil

water content was almost at the 15-bar percentage. On the other hand many investigations have shown that transpiration rate declines considerably before the 15-bar percentage in the soil is approached, e.g., the work of Schneider and Childers (1941), Loustalot (1945), Halstead (1954), Makkink and Van Heemst (1956), Slatyer (1956), Hagan et al. (1957), Lemon et al. (1957), Pierce (1958), and Scholte Ubing (1959), to mention but a few. Unfortunately, many of the experiments designed to investigate this aspect of transpiration seem to have paid little heed to the influence of either weather conditions or soil type on the results. However, some general conclusions can be reached from consideration of these experiments:

1. Under some weather conditions, transpiration rate declines at relatively high soil moisture contents, while under other weather conditions, transpiration rate is little affected by soil moisture content until the 15-bar percentage is reached.
2. For a given set of weather conditions, transpiration rate declines relatively rapidly in some soils when the average soil suction exceeds a value of 1-3 bars, while in other soils, transpiration rate remains unchanged until the average soil suction approaches 15 bars.
3. The soil moisture content at which plants wilt in

the field is not constant, but depends on the prevailing weather conditions and the soil type.

It is believed that many of these results can be explained by consideration of the dynamic aspects of transpiration as outlined in the preceding paragraphs.

EXPERIMENTAL

General

A field experiment was conducted in which the transpiration rates of corn plants growing under different soil moisture regimes and under different weather conditions were determined.

With deep-rooted crops, such as corn, there are several difficulties involved in conducting field experiments in which soil moisture content is a treatment variable. One difficulty is the fact that it is impossible to moisten dry soil in a profile to any uniform moisture content other than field capacity. As water moves through a profile, it advances in a wetting front. The soil immediately adjacent to the water must be wetted to field capacity before the excess gravitational water moves down to wet the next soil layer, and so on. Consequently, the only way to attain a certain moisture content less than field capacity is to allow plants to deplete the soil water content to that value. If one starts with a soil profile moistened to field capacity at the start of the growing season, and if rain is prevented from reaching the soil, transpiration rates are of such small magnitude that depletion of soil moisture content to any appreciable extent requires several weeks.

Again, plants growing in the field normally have a well-

developed root system near the soil surface and a rather sparse root system at depth. As water is withdrawn from the soil through transpiration, it is generally withdrawn first from the soil near the surface and then is removed from deeper and deeper soil layers. Capillary conductivities of soil are so small that movement of water between the moist and the dry regions of the profile is very slow. (Water movement in the unsaturated condition takes place at the rate of only a few millimeters a day.) Consequently, large gradients of soil moisture throughout the soil profile occur. Under these circumstances, a figure denoting the average soil moisture content or the average soil suction in the profile has little meaning.

Thus, in order to attain a sufficiently rapid rate of soil water depletion, and in order to achieve reasonable uniformity of soil moisture throughout the root zone, one must restrict the volume of soil available to the roots. This was accomplished in the present experiment by growing plants in large containers filled with soil.

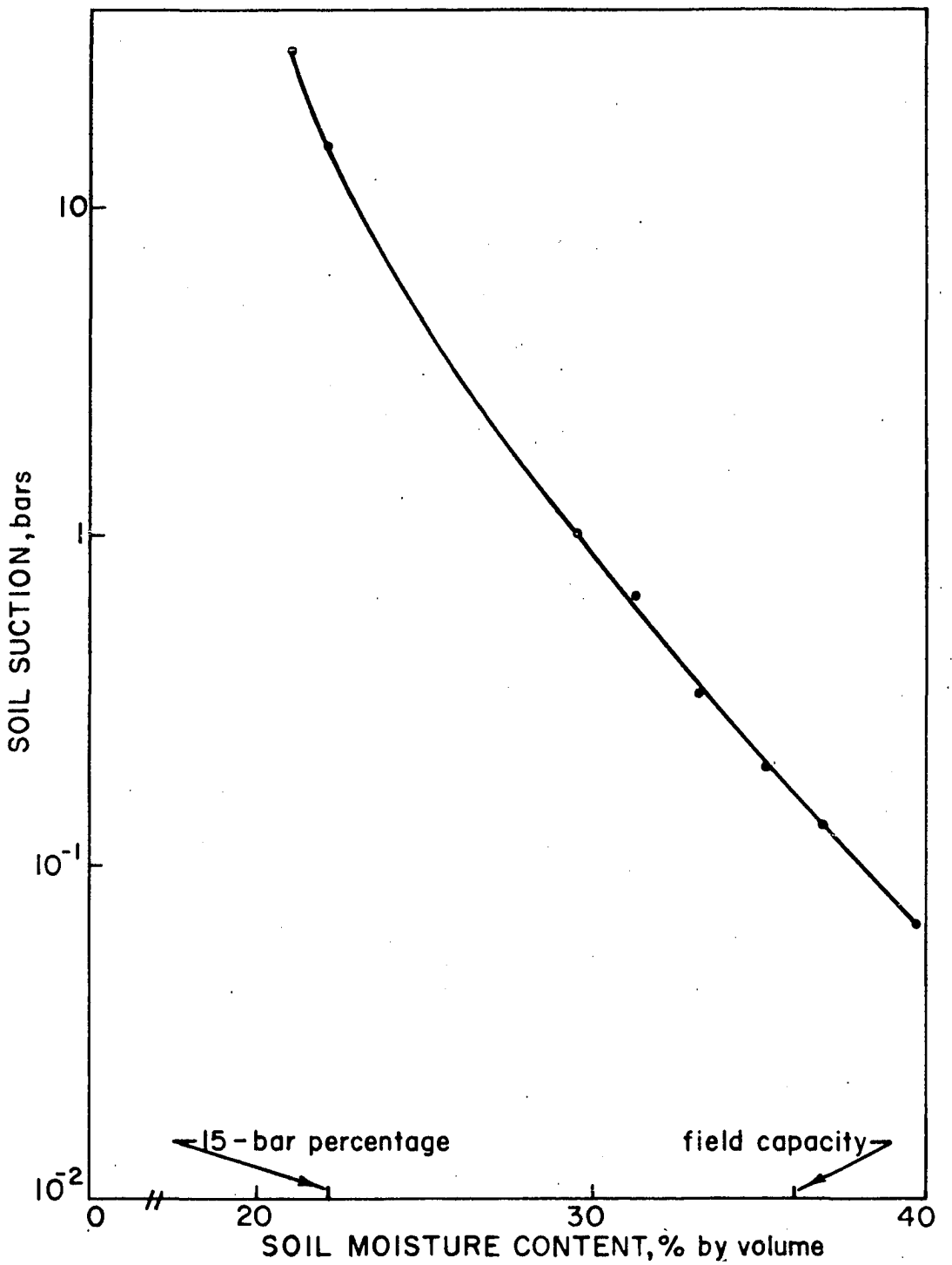
The containers, 18 inches in diameter and 24 inches in depth, were set in the field with their tops level with the surface of the ground at a spacing of 40 inches from center to center. Hills of corn, four plants to a hill, were raised in each container. Field-grown corn, also in 40-inch hills, was raised on all sides. There were 136 containers.

Soil

The soil with which the experiment was performed is a Colo silty clay loam. Field capacity for this soil is 36% by volume and the 15-bar percentage is 22% by volume. The relationship between soil moisture content and soil suction is shown in Figure 2. The soil moisture-suction determinations were made with pressure membrane apparatus. The low suction determinations were performed with small lucite pressure units described by Nielsen (1958). Undisturbed soil cores, taken from the containers, were used for the determinations. The high suction determinations were performed with conventional pressure membrane apparatus similar to that described by Richards (1947), using disturbed soil samples. Reference to Figure 2 will disclose that, of the water held in the soil between field capacity and the 15-bar percentage, more than half is held at suction values greater than 1 bar and almost 40% is held at suction values greater than 2 bars.

As the containers were set in the field, the soil dug from each hole was mixed and replaced in the container, so that the containers were filled with a reasonably uniform mixture of soil from the top two feet of the profile. As the containers were filled, the soil was packed lightly to an average bulk density of 1.07. Since the containers were made of galvanized steel, they were lined with polyethylene plastic film before filling to prevent any possible toxic

Figure 2. Relation between soil suction and volumetric soil moisture content, Colo silty clay loam


10
1
10^{-1}
10^{-2}
SOIL SUCTION, bars
15 - bar percentage
field capacity
0
20
30
40
SOIL MOISTURE CONTENT, % by volume

effects from the galvanizing. At the time of filling, an access pipe for the probe of a neutron meter was inserted in each container. An outlet was provided in the bottom of each container to allow for drainage of possible excess water.

Cultural Practices

After the containers were filled, they were watered fully and allowed to drain to field capacity. Corn was planted in the containers and in the surrounding border rows on May 26, 1959. Four corn plants were raised in each container to simulate a field population of 16,000 plants per acre. Fertilizer was applied prior to planting and further fertilizer was applied at intervals during the growing season. After the plants had emerged, the soil surface was covered with black plastic film to prevent evaporation of water from the soil surface.

As the plants grew, watering was accomplished by pumping water from a large storage tank at the experimental site. The pump was calibrated frequently so that known quantities of water could be applied to each container. The pumping rate was fairly constant although, at times, an obvious malfunction in the pump led to a variation in pumping rate with a consequent error in the estimate of the amount of water applied and a corresponding error in the estimate of transpiration rate. Until the treatments involving variation in

the soil moisture regime were imposed, the soil in all containers was maintained as close as possible to field capacity by application of water at appropriate intervals.

Determination of Soil Moisture Content and Transpiration Rate

Soil moisture content was determined by the neutron scattering technique using a commercial model of a neutron meter manufactured by Nuclear-Chicago. The neutron meter consisted of a portable scaler, Model 2800, and a depth moisture probe, Model P19. During the period in which transpiration rates were measured, soil moisture readings were made daily between the hours of 1600 and 1800. The moisture contents reported in later sections are averages for the effective root depth of the plants in the containers, which was 21 inches. Examination of root distribution after the experiment was concluded showed that the roots had permeated the soil in the containers thoroughly, except for a small zone of about 1 inch at the bottom of the container. Since the root zone was restricted, the rate of soil moisture depletion was more rapid than is the case under field conditions. Consequently, the water was depleted from the various depths in the container at a fairly uniform rate; gradients in soil moisture content from top to bottom of the containers were small.

Transpiration rates were calculated by adding the amount

of applied irrigation water to the change in soil moisture content and dividing the sum by the ratio of the ground area normally occupied by one hill of corn in the field to the ground area of the container. The value of this ratio was 6.3. The fact that the rate of water withdrawal in the containers was 6.3 times the rate in the field made it possible to deplete soil moisture content to low values in a matter of a few days. It also made it possible to measure daily transpiration rates with considerably more precision than is possible in the field, where the standard error of a difference in soil water content over a period of one day is about equal in magnitude to the daily transpiration.

Experimental Design

The experiment was designed to determine the effects of various soil moisture regimes on transpiration rate, growth rate and final grain yield. For this purpose it was conducted in two sections.

The subject matter of this thesis is the availability of soil water for transpiration. The portions of the experiment dealing with the growth responses of the plants will be referred to only in so far as they relate to this general topic. Nevertheless, the author considers it desirable to present the design of the experiment in detail so that the reader will appreciate the sources of some of the data

referred to in later sections of this thesis.

Section 1 - soil moisture depletion and net assimilation rate

In Section 1, the treatments consisted of the depletion of soil moisture content, at regular intervals during some 5 weeks of the growing season, to values corresponding to soil suctions of 2.5, 5 and 15 bars. The 5-week period commenced just prior to tasseling and extended through silking into the stage of grain development. Depletion of soil moisture was accomplished by withholding irrigation.

This section of the experiment was designed for the purpose of fitting a polynomial response surface with two x-variables, soil suction and time, to the net assimilation rate, NAR[1]. A central composite design, similar to those described by Cochran and Cox (1957, pp. 342-353), was chosen. The design was centered around a soil suction of 5 bars at the estimated date of 50% silking, August 1. The star design chosen is shown schematically in Figure 3.

When the soil suction reached the particular value specified in the design, the plants receiving the treatment

---

[1]NAR is a measure of the rate of dry matter production of a plant. It is the rate of increase of dry weight per unit leaf area. Thus,

$$NAR = \frac{1}{\bar{A}} \left(\frac{W_2 - W_1}{t_2 - t_1}\right)$$

where $\bar{A}$ is the mean leaf area of the plant between times t_2 and t_1, and W_2 and W_1 are the dry weights of the plant at times t_2 and t_1. NAR is commonly expressed in units of g. dry matter per dm^2 leaf area per day.

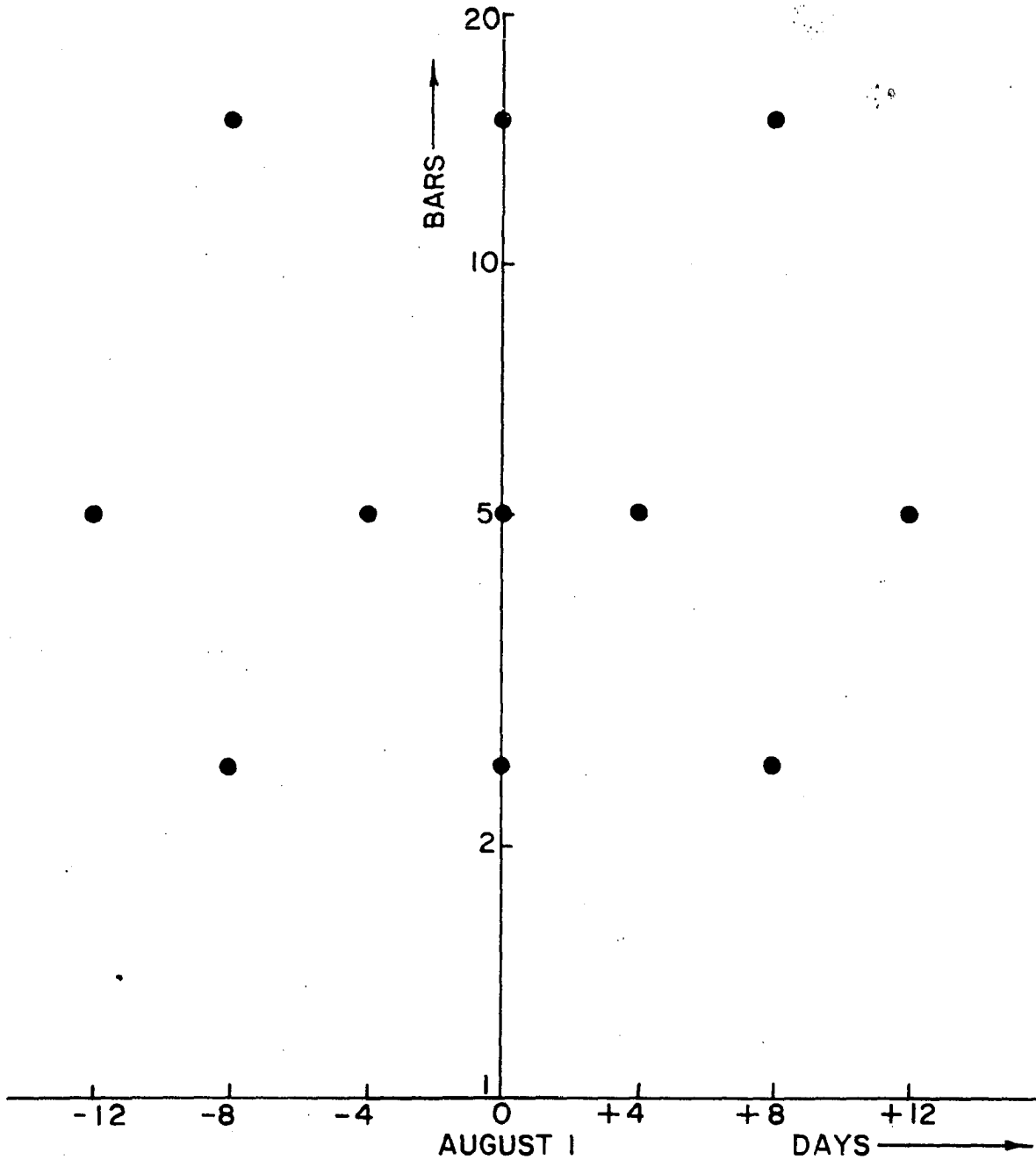


Figure 3. Central composite design for section 1. The center of the time scale, August 1, is the estimated date of 50% silking. Each point represents the time at which soil suction was to attain the value shown

in question were harvested and their dry weight was determined. Determinations of leaf area, stalk height and ear length, as well as observations as to whether or not the plants were tasseled and silked, were also made. In order to estimate the effects of the various treatments on NAR, control plants in which soil suction was not allowed to exceed a value of 0.5 bar, were also included in the experiment. The experimental procedure called for one group of control plants to be harvested at each of the seven dates on which the soil moisture treatments were to be harvested. Thus, there was a total of 18 treatments comprising 7 controls and 11 variable soil moisture treatments in the experiment. The basic design was replicated four times.

The NAR for each treatment was calculated for the period during which irrigation was withheld. The NAR of the control plants over the same period was also calculated. Then, the effect of each treatment on NAR could be obtained by calculating its relative NAR, i.e., the ratio of the NAR of the treatment to the NAR of the control plants over the same period.

In practice, it was found impossible to have soil moisture depleted to the specified level on the date called for in the original design of the experiment. Variations in weather conditions and the reduction in transpiration rate with declining soil moisture content made it impossible to predict the transpiration rate and the corresponding rate of water

withdrawal from the soil. The actual dates on which the soil moisture contents were depleted to the specified levels and the dates on which the control plants were harvested are shown in Table 1. The dates shown in Table 1 are the mean dates for the four replications.

Section 2 - soil moisture depletion and grain yield

Section 2 of the experiment was designed for the purpose of fitting a polynomial response surface with two x-variables, soil suction and time, to final grain yields. A central composite design, similar to that employed in Section 1, but with the addition of two points, was chosen. The planned design is shown in Figure 4. The effects of the soil moisture treatments on grain yield were estimated by calculating relative grain yields, i.e. the ratio of the yield of grain for the particular treatment to the yield of grain of control plants. For this purpose, three groups of control plants were included in the experiment. The soil suction in the controls was not allowed to exceed 0.5 bar. There were a total of 16 treatments, comprising 3 controls and 13 variable soil moisture treatments, in the experiment. The basic design was replicated four times.

After the soil suction in each treatment had attained the specified value, the soil was irrigated to field capacity and the soil suction was not allowed to exceed 0.5 bar for

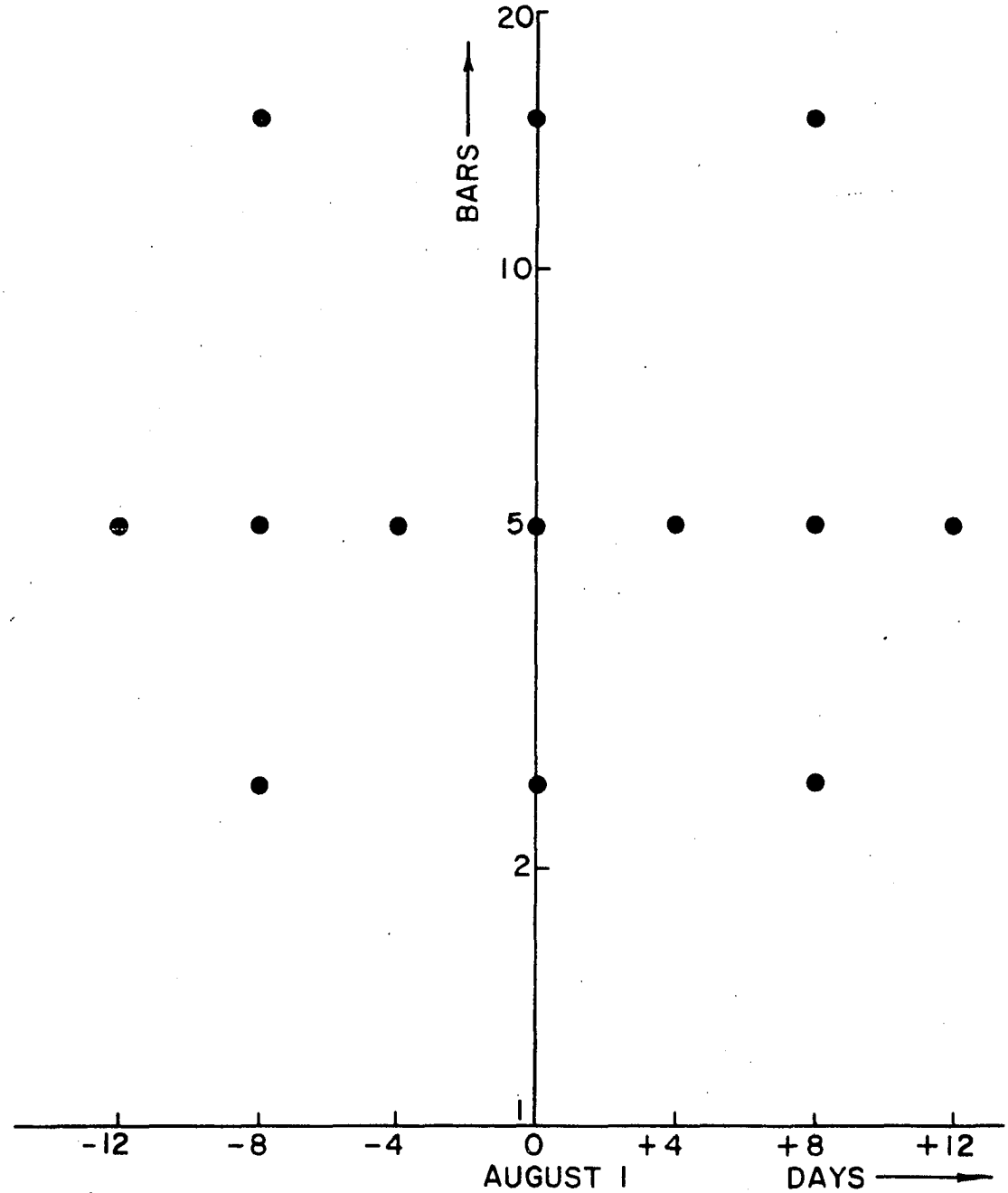


Figure 4. Central composite design for section 2. The center of the time scale, August 1, is the estimated date of 50% silking. Each point represents the time at which soil suction was to attain the value shown

Table 1. Actual dates on which soil suction attained the value specified in the experimental design, Section 1

Soil suction	Date specified by the design						
	July 20	July 24	July 28	Aug. 1	Aug. 5	Aug. 9	Aug. 13
2.5 bars		July 23		Aug. 2		Aug. 10	
5 bars	July 21		Aug. 1	Aug. 3	Aug. 9		Aug. 14
15 bars		July 27		Aug. 7		Aug. 14	
Harvest date of control plants	July 21	July 25	Aug. 1	Aug. 3	Aug. 9	Aug. 10	Aug. 14

the remainder of the growing season.

Again it was not possible to have the soil moisture depleted to the specified level on the dates called for by the design. The actual dates on which the specified value of suction was attained are shown in Table 2. The dates shown in Table 2 are the mean dates for the four replicates.

Transpiration rate

As previously mentioned, soil moisture content was determined daily during the period in which the soil moisture treatments in sections 1 and 2 were applied. The treatments were so arranged that on each day during the 5-week period there were a number of containers at different soil moisture contents ranging from field capacity to the 15-bar percentage. The soil moisture data from these containers were used to calculate daily transpiration rates. In this way, the combined effects of daily variations in weather conditions and variations in soil moisture content on transpiration rate could be studied. This information was then used to verify the theoretical predictions concerning transpiration discussed in the introductory section.

Table 2. Actual dates on which soil suction had attained the value specified in the experimental design, section 2

Soil suction	Date specified by the design						
	July 20	July 24	July 28	Aug. 1	Aug. 5	Aug. 9	Aug. 13
2.5 bars		July 24		Aug. 3		Aug. 10	
5 bars	July 21	July 24	July 28	Aug. 7	Aug. 11	Aug. 11	Aug. 14
15 bars		July 26		Aug. 6		Aug. 12	

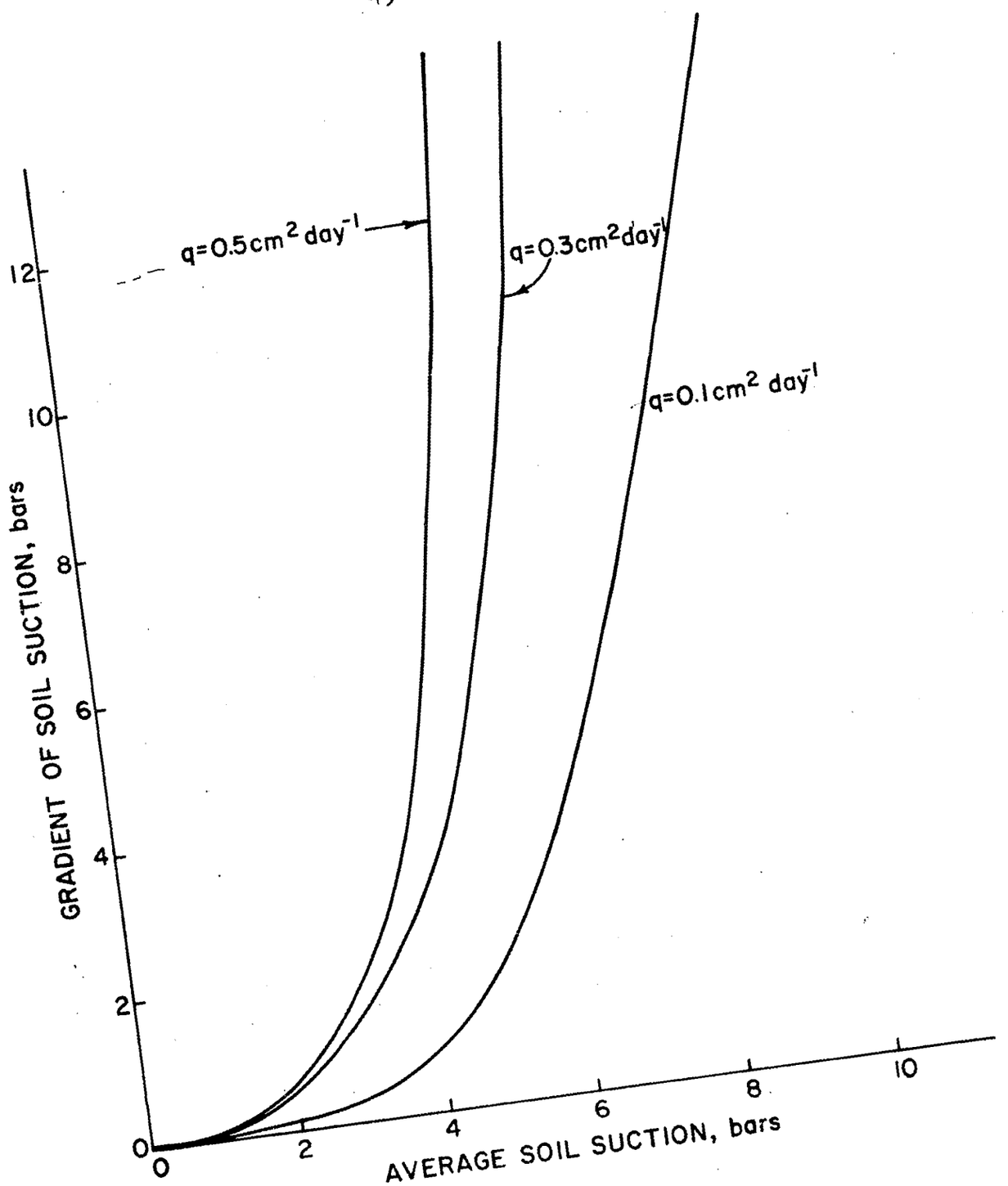
RESULTS AND DISCUSSION

Actual Transpiration Rate

Theoretical

In examining the solution of the flow equation, Equation 8, it was found that the gradient of soil suction required to produce a given transpiration rate or a given flux rate of water to the root, is a function of the water uptake rate q, the capillary conductivity of the soil K, the diffusivity for soil water flow D, the root radius a, and the time t. It was shown that the value of the suction gradient $\Delta\psi$, is relatively insensitive to variations in D and a. By assuming some typical constant values for these factors, and by examining the solution after the elapse of a certain period of time, for which t = 1 day is an appropriate time interval, we can examine the change in $\Delta\psi$ as q is varied. Variations in the values of D and a will not materially affect the results. The results of such calculations are presented in Figure 5, where the value of $\Delta\psi$ required to produce a given value of q (or a given value of T, the transpiration rate) is shown as a function of the average soil suction in the root zone, for three values of q. The range in the values of q shown in Figure 5, viz., 0.1 to 0.5 $cm.^2\ day^{-1}$, covers the range likely to be encountered under field conditions (Ogata *et al.*, 1960). The values of K used in the calcula-

Figure 5. Gradient of soil suction (from the boundary of the region of influence of the root to the surface of the root) required to produce a given rate of water uptake q, as a function of the average soil suction in the root zone


q=0.5cm² day⁻¹
q=0.3cm² day⁻¹
q=0.1cm² day⁻¹
GRADIENT OF SOIL SUCTION, bars
AVERAGE SOIL SUCTION, bars
0
2
4
6
8
10
12

tions were obtained from data of Gardner (1960). A constant value of 7 for the term $\ell n \frac{4Dt}{a^2} - \gamma$ was assumed.

Figure 5 shows that at low values of soil suction, the gradient of suction required to produce a given flux rate is small. As soil suction increases and the value of K decreases, the gradients required to move soil water to the root increase appreciably. When ψ has an average value of 5 bars, a gradient of 10 bars suction from the boundary of the region of influence of the root to the root surface is required to produce a flux rate of 0.5 cm.^{2} day^{-1}. Smaller values of $\Delta\psi$ are required to produce slower flux rates. When the average soil suction exceeds 5 bars, impossibly large gradients (from the point of view of the plant) are required to move water to the root at the rapid flux rates. Only the smaller flux rates are possible. When the average value of soil suction exceeds 10 bars, even the very slow flux rates require very large gradients of suction.

By making certain assumptions, solutions of the flow equation can be used to predict the actual transpiration rate at any value of soil suction in the root zone and for any given potential transpiration rate. First, we assume that there is an upper limit to the transpiration rate from a plant, which is determined by the maximum DPD in the leaves. Second, we simplify transpiration by assuming that there is no difference in DPD from leaf to leaf, and that evaporation

is occurring from all leaves at the same rate. Third, we assume that transpiration rate is directly proportional to the gradient in DPD from leaf to root and that the permeability of the plant to water flow remains essentially constant. Under these assumptions, we can write

$$T = k\,\Delta DPD = k(DPD_{leaf} - DPD_{root})$$

where T is the transpiration rate and k is the permeability (or conductivity) of the plant for water flow, and

$$T_{FC\ max} = k(\Delta DPD)_{FC\ max} = k(DPD_{leaf\ max} - DPD_{root\ FC})$$

where $T_{FC\ max}$ is the maximum transpiration rate for a plant growing in soil at a moisture content of field capacity, $(\Delta\,DPD)_{FC\ max}$ is the gradient from leaf to root when the DPD in the leaf is at its maximum value, $DPD_{leaf\ max}$, and the DPD in the root is at its lowest value, $DPD_{root\ FC}$, which is the DPD in the root when the soil adjacent to the root is at field capacity.

For purposes of illustration, a value of 25 bars was assumed for the maximum DPD in the leaf and a value of transpiration equivalent to a flux rate to the root of 0.5 $cm.^2\ day^{-1}$ was assumed for $T_{FC\ max}$. Solution of Equation 8 for $\Delta\psi$, when ψ_o has a value corresponding to field capacity, K has the value appropriate to ψ_o, and q has a value of 0.5 $cm.^2\ day^{-1}$, yields a value of 0.2 bar for the value of ψ

at the root surface. Thus,

$$T_{FC} = k(25 - 0.2) = 24.8k$$

Solution of the equation when ψ_o has increased to 5 bars, and assuming in the first instance that q is still equal to 0.5 $cm.^2\ day^{-1}$, yields a value of 15 bars for the value of at the root surface. Thus,

$$T = k(25 - 15) = 10k$$

and

$$T/T_{FC} = 10k/24.8k = 0.4$$

Now, if T/T_{FC} is equal to 0.4, then q/q_{FC} must also equal 0.4, i.e., the rate of flow of water to the root must equal the rate at which water is being transpired. Thus, it was necessary to solve again for Δ DPD and then for T/T_{FC}, when q/q_{FC} equals 0.4, and so on until repeated solution yields a value of T/T_{FC} equal to q/q_{FC}. In this instance, the appropriate value of T/T_{FC} is 0.57. By repeated solution in this way, the relative transpiration rate can be calculated as a function of the average soil suction in the root zone.

When weather conditions are such that T_{FC} is smaller than $T_{FC\ max}$, the following relationship holds:

$$\frac{T_{FC}}{T_{FC\ max}} = \frac{(\Delta\,DPD)_{FC}}{(\Delta\,DPD)_{FC\ max}}$$

Thus, $\Delta\ DPD_{FC}$ will be smaller than $\Delta\ DPD_{FC\ max}$ and the value of DPD in the leaf when the soil is at field capacity will

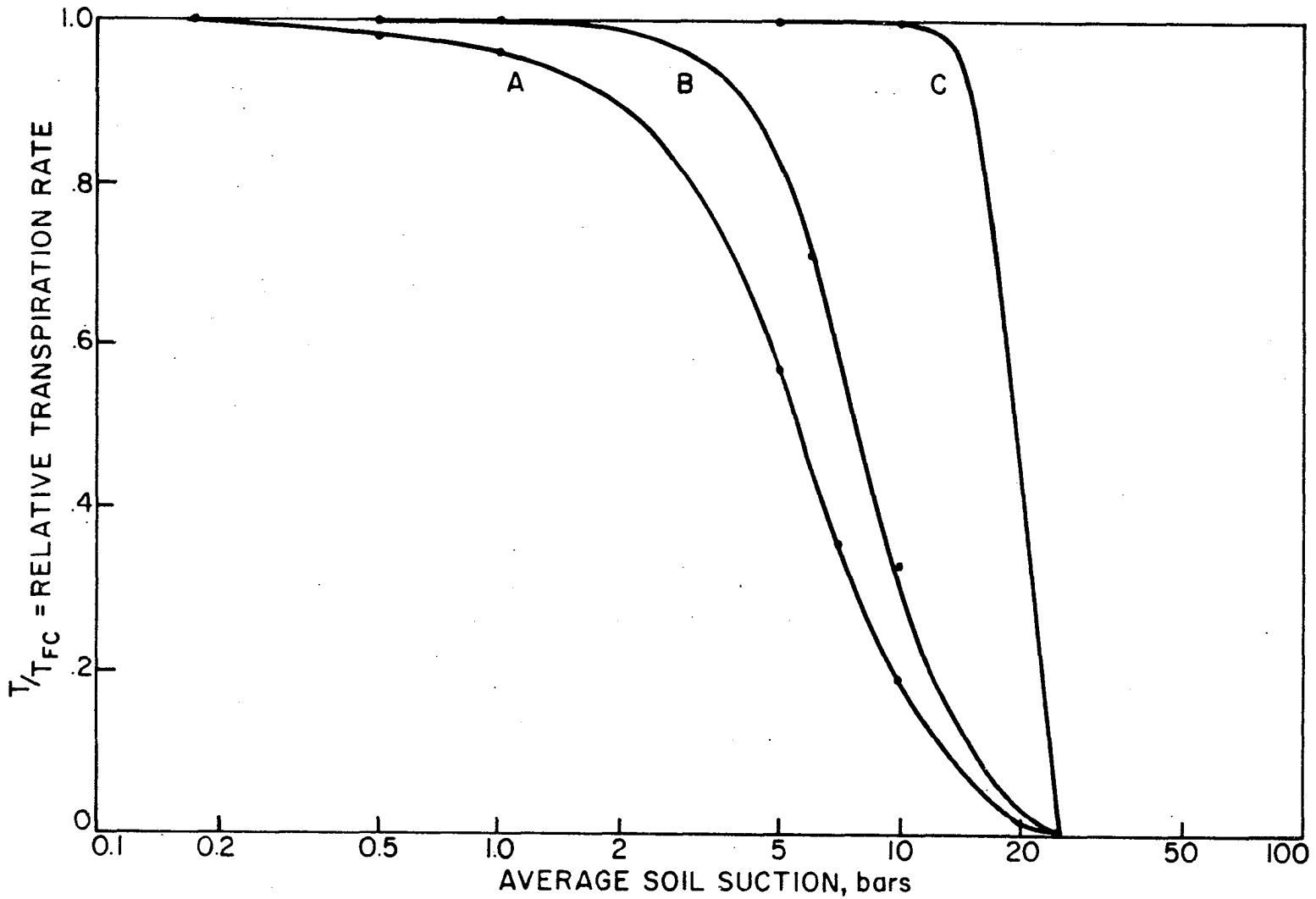
be less than the maximum value of 25 bars. As ψ_o increases, the value of ψ at the root increases, and for T to be equal to T_{FC}, the DPD in the leaf must also increase so that Δ DPD equals Δ DPD_{FC}. When the DPD in the leaf has attained the value of 25 bars, Δ DPD becomes less than Δ DPD_{FC} and T becomes less than T_{FC}. As in the previous case where T_{FC} was equal to $T_{FC\ max}$, repeated solution for Δ DPD enables calculation of relative transpiration rate as a function of the average soil suction.

Figure 6 shows the results of such calculations, assuming a value of $T_{FC\ max}$ equivalent to a value of q_{FC} of 0.5 $cm.^2$ day^{-1}, and assuming values of K suggested by the data of Gardner (1960). Figure 6 indicates that actual transpiration rate does not differ appreciably from the transpiration at field capacity until the average value of soil suction exceeds a value of 2 bars. Thereafter, with high potential transpiration conditions, transpiration rate decreases rapidly with increasing soil suction. When low potential transpiration conditions prevail, the actual transpiration rate does not decrease significantly until the average soil suction approaches a value of 15 bars.

Experimental

The data from the field experiment provided information for calculation of the actual transpiration rate for a range

Figure 6. Relative transpiration rate as a function of the average soil suction in the root zone, when the maximum transpiration rate possible corresponds to a value of water uptake rate by the roots of 0.5 $cm^2 day^{-1}$, and the maximum DPD which can be developed in the plant is 25 bars. The curves shown represent three different potential transpiration conditions: A, when the transpiration rate at field capacity T_{FC} corresponds to a water uptake rate by the roots q_{FC} of 0.5 $cm^2 day^{-1}$; B, when T_{FC} corresponds to a value of q_{FC} of 0.3 $cm^2 day^{-1}$; C, when T_{FC} corresponds to a value of q_{FC} of 0.1 $cm^2 day^{-1}$


1.0
.8
.6
.4
.2
0
A
B
C
T/T_{FC} = RELATIVE TRANSPIRATION RATE
0.1
0.2
0.5
1.0
2
5
10
20
50
100
AVERAGE SOIL SUCTION, bars

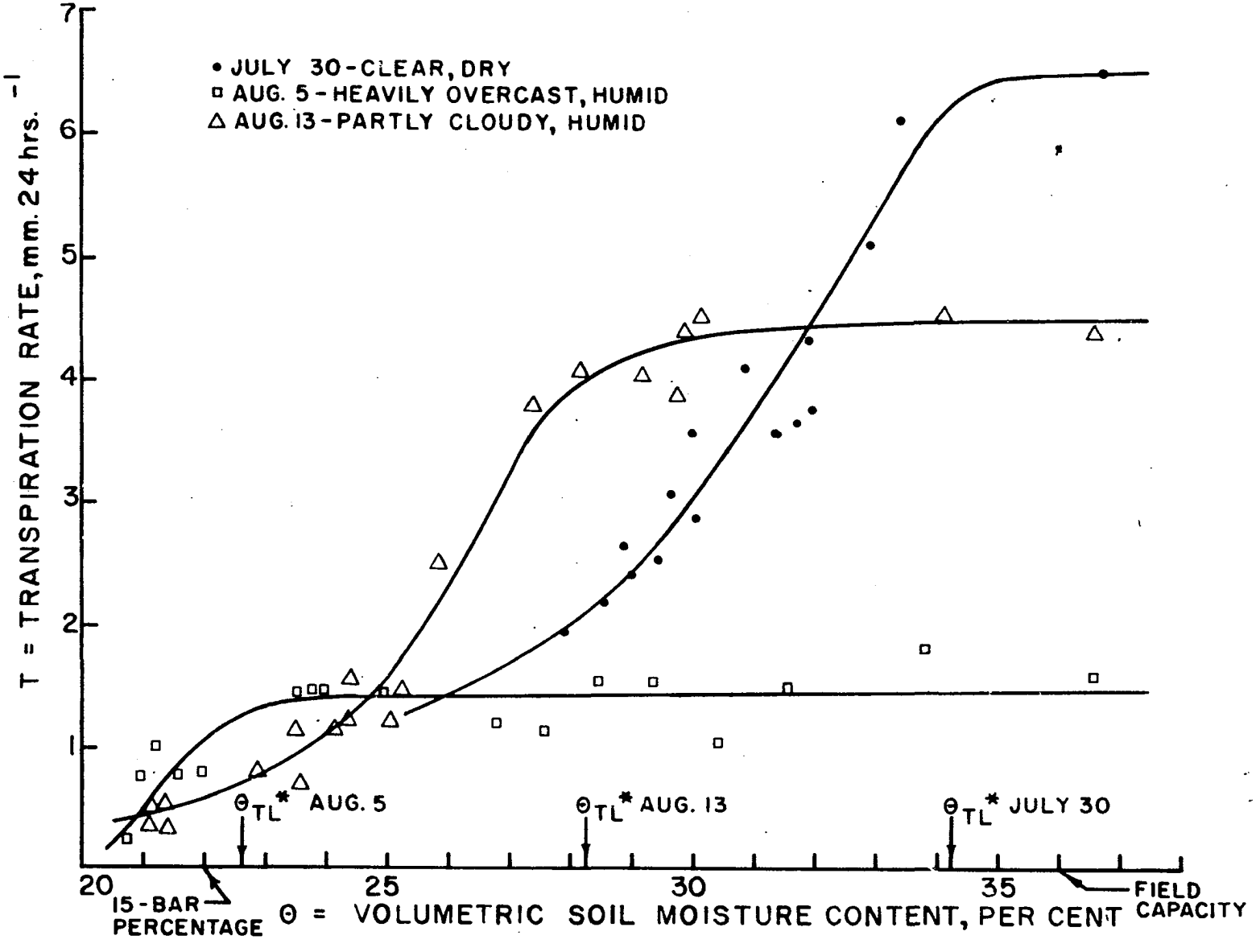
of soil moisture conditions on each of 25 different days. In this way, the course of transpiration could be followed over a range of different soil moisture regimes and over a variety of weather conditions which imposed a variety of potential transpiration rates. Actual transpiration rate T was plotted as a function of soil moisture content θ on each of the days. The number of containers represented by the points plotted for any one day varied, but was never less than 15. The relationship between T and θ on three of the days is shown in Figure 7. The days, July 30, August 13 and August 5, represented respectively, clear dry conditions, partly cloudy humid conditions, and heavily overcast conditions.

The transpiration rate at field capacity T_{FC} was determined by meteorological conditions as discussed in the introductory section. The relationship between T_{FC} and meteorological conditions will be further examined in a later section. For our present purpose, we can take it that T_{FC} represents the potential transpiration rate.

When T_{FC} was high, as on July 30, T fell below T_{FC} when θ had decreased a little below field capacity. When T_{FC} was low as on August 5, T did not fall below T_{FC} until θ had decreased almost to the 15-bar percentage.

Among the 25 different days examined, days similar to each other in meteorological conditions and in the value of

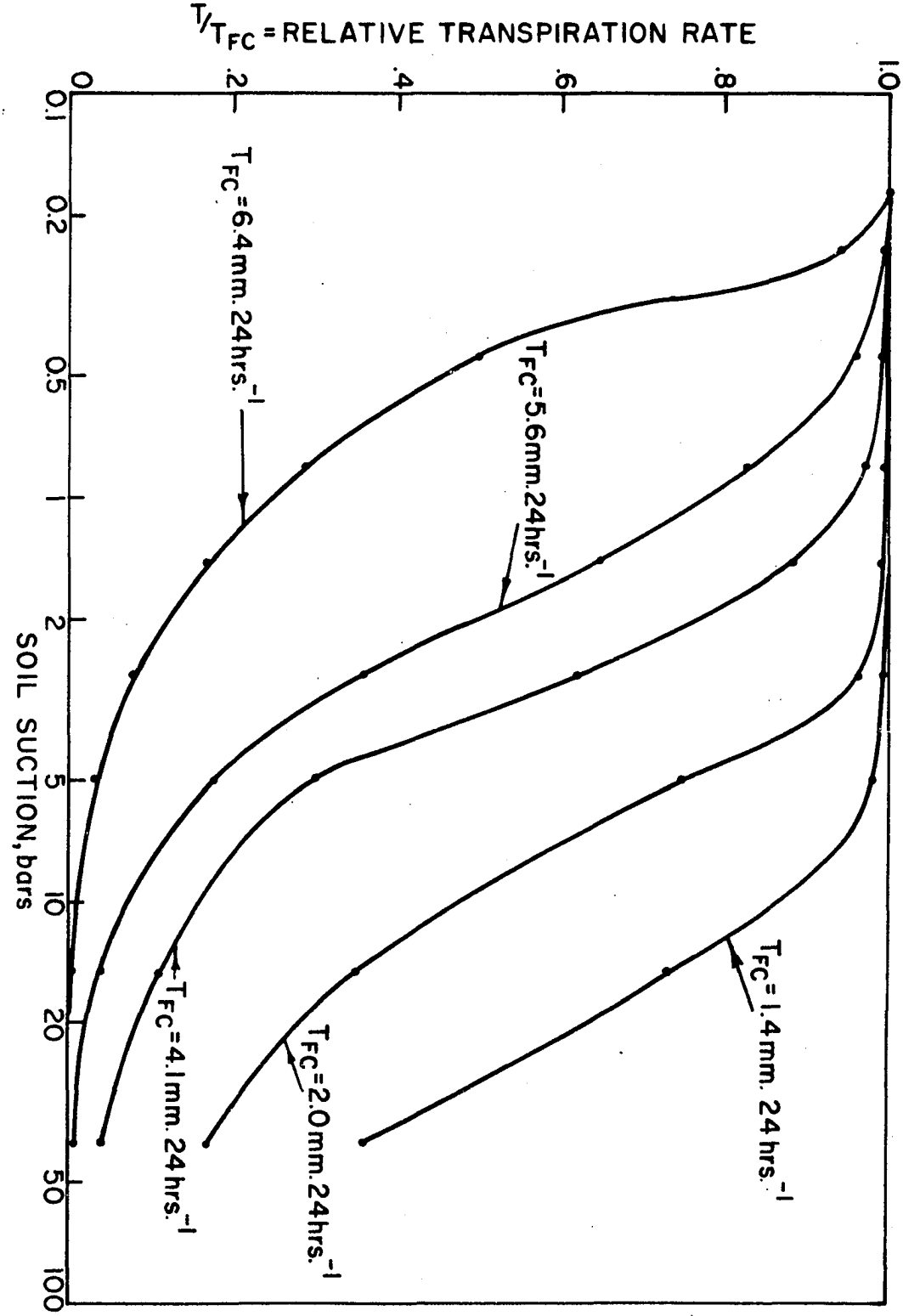
Figure 7. Actual transpiration rate as a function of soil moisture content for Colo silty clay loam


• JULY 30 - CLEAR, DRY
□ AUG. 5 - HEAVILY OVERCAST, HUMID
△ AUG. 13 - PARTLY CLOUDY, HUMID
T = TRANSPIRATION RATE, mm. 24 hrs.⁻¹
7
6
5
4
3
2
1
θTL* AUG. 5
θTL* AUG. 13
θTL* JULY 30
20
25
30
35
15-BAR PERCENTAGE
FIELD CAPACITY
θ = VOLUMETRIC SOIL MOISTURE CONTENT, PER CENT

T_{FC} were encountered. These days were grouped into classes according to the value of T_{FC}; then the mean relative transpiration rate T/T_{FC} was calculated for each class for selected values of θ and selected values of soil suction between field capacity and the 15-bar percentage. The relationship between T/T_{FC} and ψ is shown in Figure 8 for different mean values of T_{FC}. For moderate to low values of T_{FC}, the data plotted in Figure 8 agree quite well with the theoretical curves plotted in Figure 6, despite the simplifying assumptions made in the calculations. At high values of T_{FC}, the decrease in relative transpiration rate is much more rapid than the calculations suggest. This discrepancy probably arises from 3 main sources:

1. The calculations assumed that there was no difference in DPD from leaf to leaf and that evaporation occurs from all leaves at the same rate. In the field, there undoubtedly is a big difference in DPD from leaf to leaf as one moves from the top to the bottom of the canopy. The top leaves of the canopy receive much more solar radiation than the bottom leaves. Measurements by Denmead et al. (1961) showed that in a corn field, the net radiation, which is the energy available for transpiration, decreased very rapidly as one moved downwards into the canopy. At about half the canopy height, the net radiation

Figure 8. Relative transpiration rate as a function of soil suction in Colo silty clay loam for different potential transpiration conditions. The curves represent days on which the transpiration rates at field capacity were equal to the values shown in the body of the figure


T/T_FC = RELATIVE TRANSPIRATION RATE
0
.2
.4
.6
.8
1.0
0.1
0.2
0.5
1
2
5
10
20
50
100
SOIL SUCTION, bars
T_FC = 6.4 mm. 24 hrs.^-1
T_FC = 5.6 mm. 24 hrs.^-1
T_FC = 4.1 mm. 24 hrs.^-1
T_FC = 2.0 mm. 24 hrs.^-1
T_FC = 1.4 mm. 24 hrs.^-1

was only some 5% of the net radiation above the crop. Thus, the top leaves would be expected to be transpiring at about 20 times the rate of the bottom leaves. One would then expect that, under high transpiration conditions, turgor would be lost very quickly in these top leaves as soon as soil moisture content decreased below field capacity. Since these leaves are contributing most to transpiration, the actual transpiration rate would then decline very rapidly.

2. The relation,

$$T = k \Delta DPD ,$$

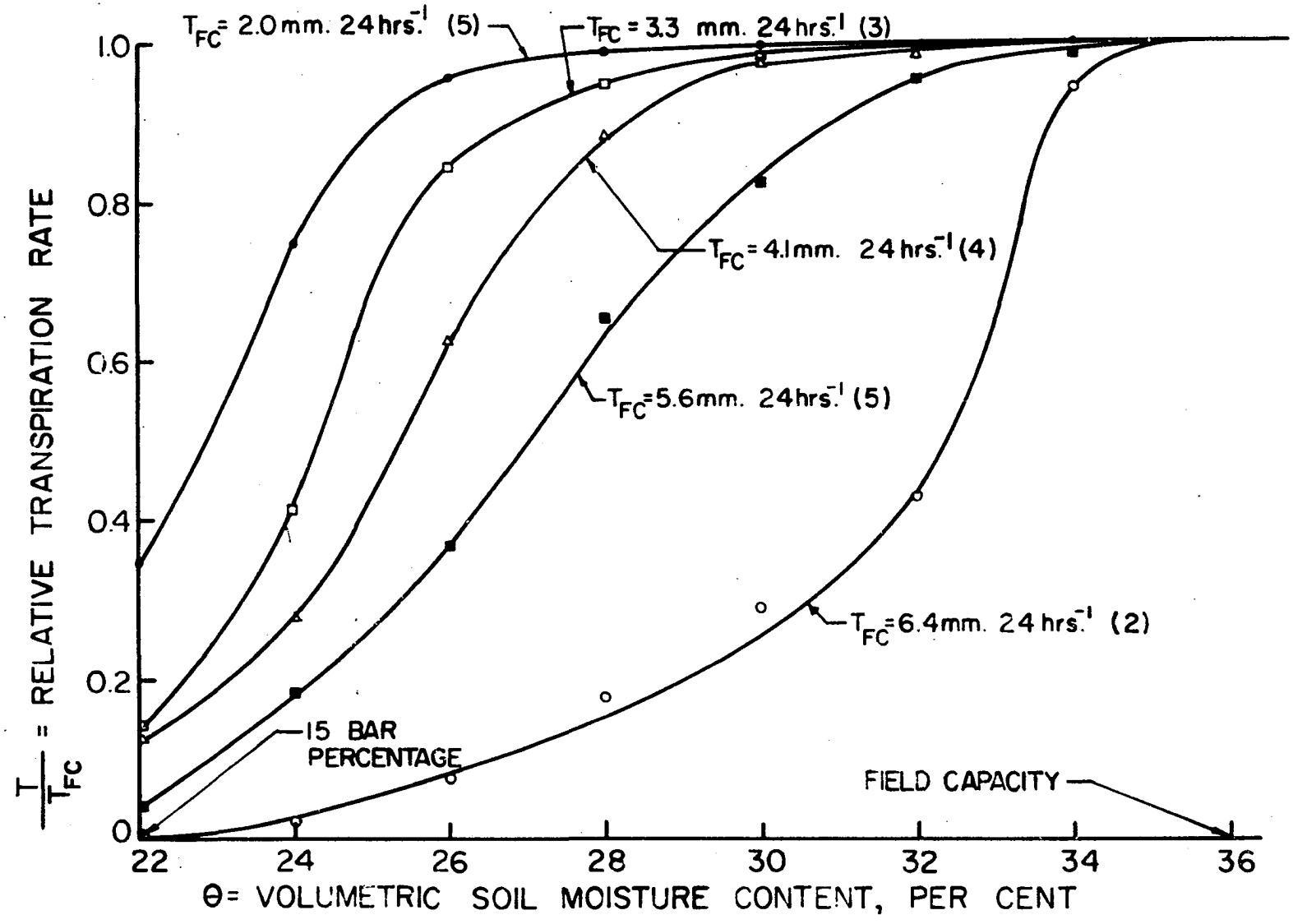
used in the calculations of relative transpiration rate, assumed that k, the permeability of the plant to water movement was constant. One would expect that the permeability of the plant might decrease as turgor is reduced. After reviewing the available literature, Slatyer (1960) states that it is probable that any marked reduction in turgor has a direct and severe inhibitory effect on permeability and hence on absorption (of water).

3. The values of capillary conductivity K used in the calculations may be somewhat higher than the corresponding values of K for the Colo soil used in the experiment.

It is evident from Figure 8 that the maximum DPD which can be developed in the leaves of corn is considerably in excess of the 25 bars assumed in the calculations. Indeed, on days when the potential transpiration rate was small, such as the days represented by the curves for a mean T_{FC} of 1.4 mm. 24 hrs.$^{-1}$, it was still possible to measure some transpiration when the average soil suction was at a value of 40 bars. For transpiration to occur, the DPD in the plant must have been considerably in excess of 40 bars. The curves in Figure 8 appear to converge to zero at a value of soil suction in the vicinity of 100 bars. Thus, one would expect that the maximum DPD which can be developed in the leaves of corn is in the neighbourhood of 100 bars. Such a value is considerably in excess of the DPD values normally considered as maximum for most plant species, but it is not an improbable value. According to Slatyer (1960), the highest values of DPD measured or estimated in plants have been about 200 bars. Slatyer (1957) reported that during an experiment in which tomato and cotton plants were subjected to increasing soil moisture stress, the DPD in the leaves of tomato approached a maximum of about 40 bars and the DPD in the leaves of cotton approached a maximum of about 100 bars.

In Figure 9, the relative transpiration rate is plotted as a function of soil moisture content. The data in Figures 8 and 9 illustrate the importance of knowing the particular

Figure 9. Relative transpiration rate as a function of soil moisture content for Colo silty clay loam for different potential transpiration conditions. The curves represent days on which the transpiration rates at field capacity had the values shown in the body of the figure. The numbers in parentheses refer to the number of observed days represented by the various curves


T_{FC}= 2.0mm. 24hrs.$^{-1}$ (5)
T_{FC} = 3.3 mm. 24hrs.$^{-1}$ (3)
T_{FC}= 4.1mm. 24 hrs.$^{-1}$ (4)
T_{FC}=5.6mm. 24hrs.$^{-1}$ (5)
T_{FC}=6.4mm. 24 hrs.$^{-1}$ (2)
15 BAR PERCENTAGE
FIELD CAPACITY
$\frac{T}{T_{FC}}$ = RELATIVE TRANSPIRATION RATE
1.0
0.8
0.6
0.4
0.2
0
22
24
26
28
30
32
34
36
Θ= VOLUMETRIC SOIL MOISTURE CONTENT, PER CENT

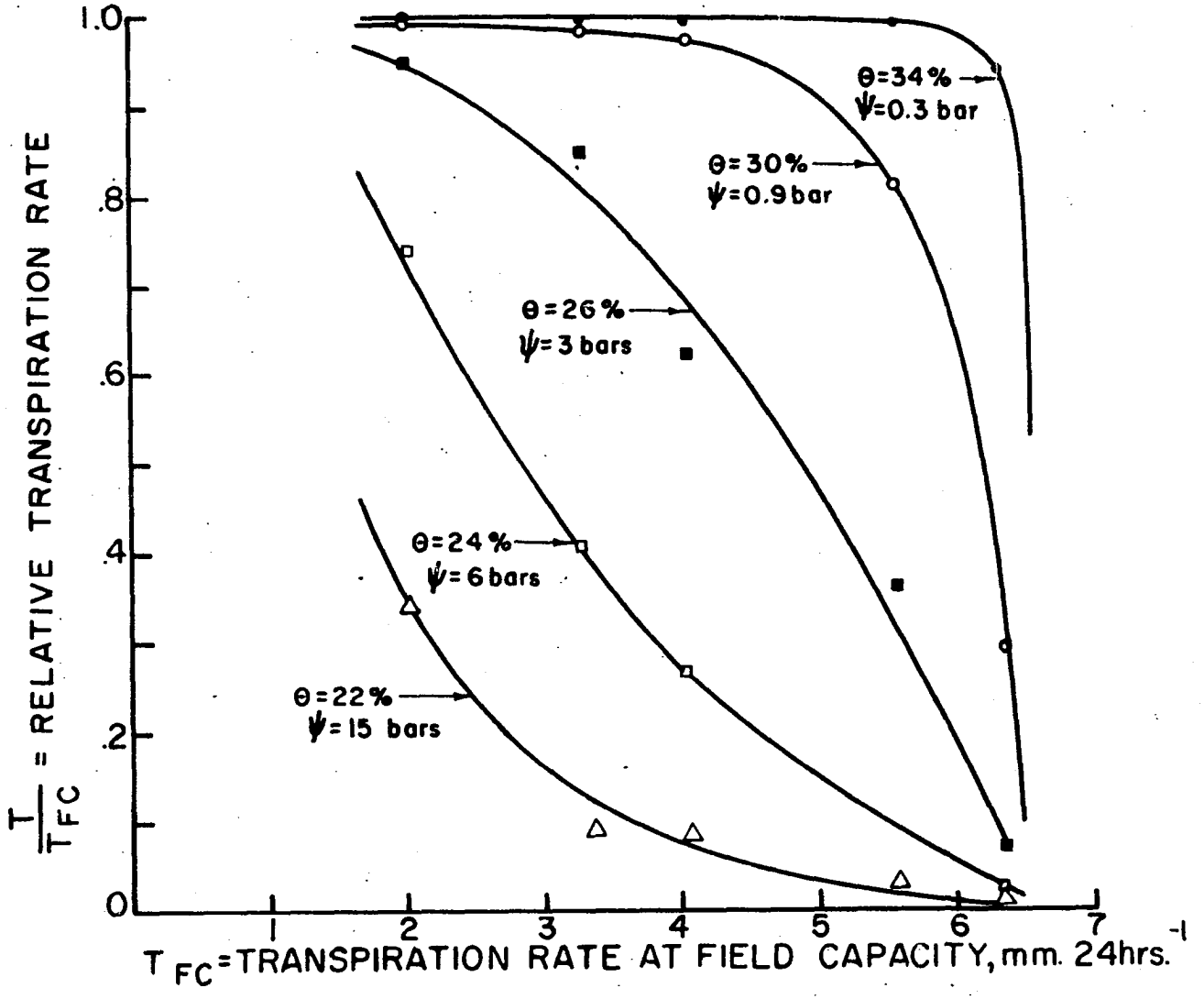
meteorological conditions (which in turn determine the potential transpiration rate) under which results have been obtained, when considering reports on the availability of soil water to plants. Under conditions leading to a high potential transpiration rate, the actual transpiration rate may be considerably less than the potential rate even though soil moisture supply would normally be considered adequate. Under conditions leading to a low potential transpiration rate, the actual transpiration rate will equal the potential rate down to very low soil moisture contents.

In Figure 10, which is a cross plot of Figure 9, relative transpiration rate is shown as a function of the transpiration rate at field capacity for selected values of soil moisture content. Again, it is obvious that the availability of soil water to the plant depends on both the potential transpiration rate and the soil moisture content (soil suction). It is interesting to observe that, if one were to extrapolate the data in Figure 10, relative transpiration rate would approach, for all soil moisture contents, a value of zero at a T_{FC} in the vicinity of 6.6 mm. 24 hrs.$^{-1}$. This does suggest that, in fact, there is an upper limit to the transpiration rate.

Influence of soil type

Although the influence of soil type was not investigated in this experiment, some data are available from Gardner

Figure 10. Relative transpiration rates at various values of soil moisture content θ and soil suction ψ as functions of the transpiration rate at field capacity

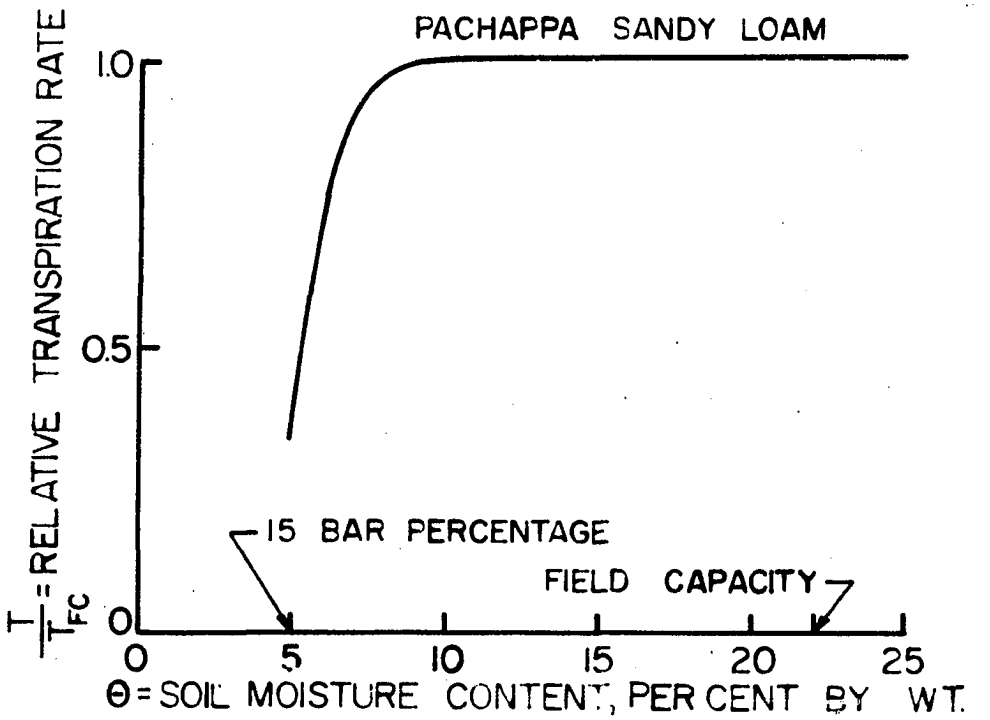

1.0
.8
.6
.4
.2
0
θ=34%
ψ=0.3 bar
θ=30%
ψ=0.9 bar
θ=26%
ψ=3 bars
θ=24%
ψ=6 bars
θ=22%
ψ=15 bars
1
2
3
4
5
6
7
T/T_FC = RELATIVE TRANSPIRATION RATE
T_FC = TRANSPIRATION RATE AT FIELD CAPACITY, mm. 24hrs.^-1

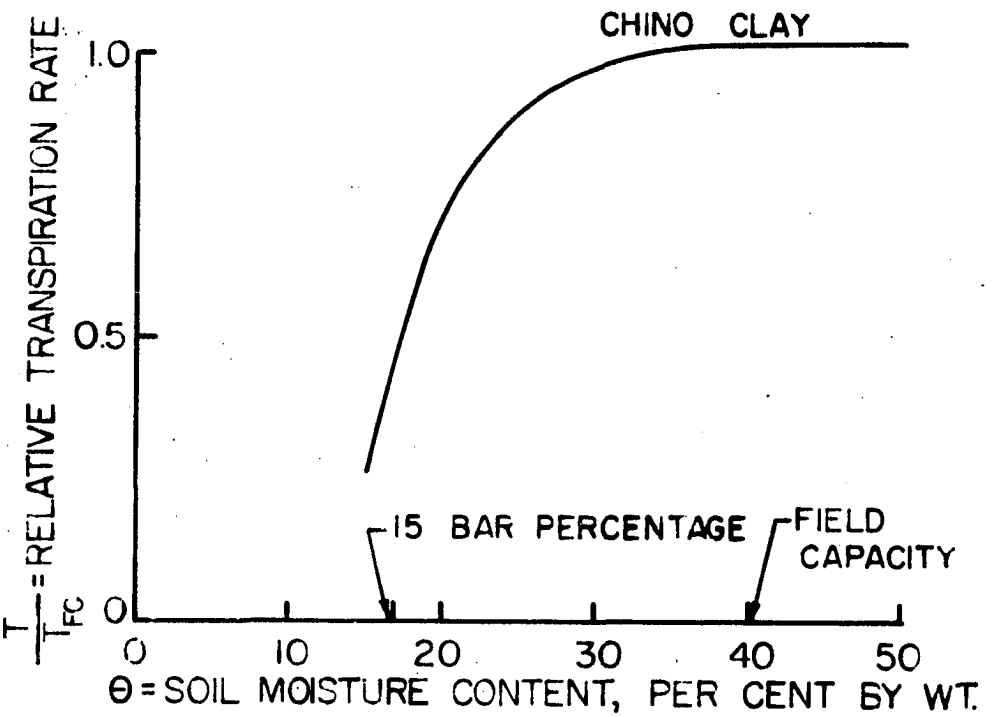
(1960). Two of Gardner's calculated curves showing relative transpiration rate as a function of soil moisture content for Pachappa sandy loam and Chino clay are shown in Figure 11. The curves were calculated for a value of q_{FC} of 0.1 cm.^{2} day^{-1}. The relationship between relative transpiration rate and soil moisture content depends primarily on the relationship between ψ and θ. There is also some dependence on the relationship between K and ψ, but Gardner's data indicate that there is little difference between the two soils in this respect. In coarse-textured soils, ψ does not increase appreciably until θ approaches the 15-bar percentage. Gardner's data indicate that in the Pachappa sandy loam, approximately 90% of the water held in the soil between field capacity and the 15-bar percentage is retained at suction values less than 2 bars. In the Chino clay, only about 60% of this water is retained at suction values less than 2 bars. In the sandy loam, the effect of decreasing soil moisture content on relative transpiration rate was insignificant until the 15-bar percentage was approached, while in the clay, relative transpiration rate declined appreciably when only a relatively small decrease in soil moisture content had occurred.

Comparison with reported observations

These considerations of the dependence of the availability of soil water on potential transpiration rate and on

Figure 11. Relative transpiration rate as a function of soil moisture content for a sandy loam and a clay (after Gardner, 1960). The curves were calculated for a rate of water uptake by the roots of 0.1 $cm^2 day^{-1}$ when the soil was at field capacity. The maximum DPD which could be developed in the plant was assumed to be 25 bars


PACHAPPA SANDY LOAM
1.0
0.5
0
$\frac{T}{T_{FC}}$ = RELATIVE TRANSPIRATION RATE
15 BAR PERCENTAGE
FIELD CAPACITY
0
5
10
15
20
25
Θ = SOIL MOISTURE CONTENT, PER CENT BY WT.


CHINO CLAY
1.0
0.5
0
$\frac{T}{T_{FC}}$ = RELATIVE TRANSPIRATION RATE
15 BAR PERCENTAGE
FIELD CAPACITY
0
10
20
30
40
50
Θ = SOIL MOISTURE CONTENT, PER CENT BY WT.

the soil moisture retention characteristics allow us to reconcile many of the apparent discrepancies in the literature concerning the availability of soil water to plants. In Figure 12, four proposals for the variation in relative transpiration rate with variation in soil moisture content are shown. Veihmeyer and Hendrickson's (1955) thesis, represented by curve A, is for equal availability of soil water from field capacity almost to the 15-bar percentage. It appears to be based largely on experiments of two types: experiments conducted on soils with moisture retention characteristics similar to those of the Pachappa sandy loam discussed in the previous section, and experiments conducted either in a greenhouse or in growth chambers, where radiation intensity, and consequently potential transpiration rate, is low. In both situations Figures 11 and 9 show that such a thesis is indeed tenable.

Pierce's (1958) proposal, curve B, is based on records obtained from a weighing lysimeter over several weeks. During this time, environmental conditions would be expected to vary widely. His curve agrees very well with those obtained under the "usual" weather conditions of a moderate potential transpiration rate pertaining in the experiment described here (see Figure 9 for comparison).

Thornthwaite and Mather's (1955) proposal for a linear relation between relative transpiration rate and "available"

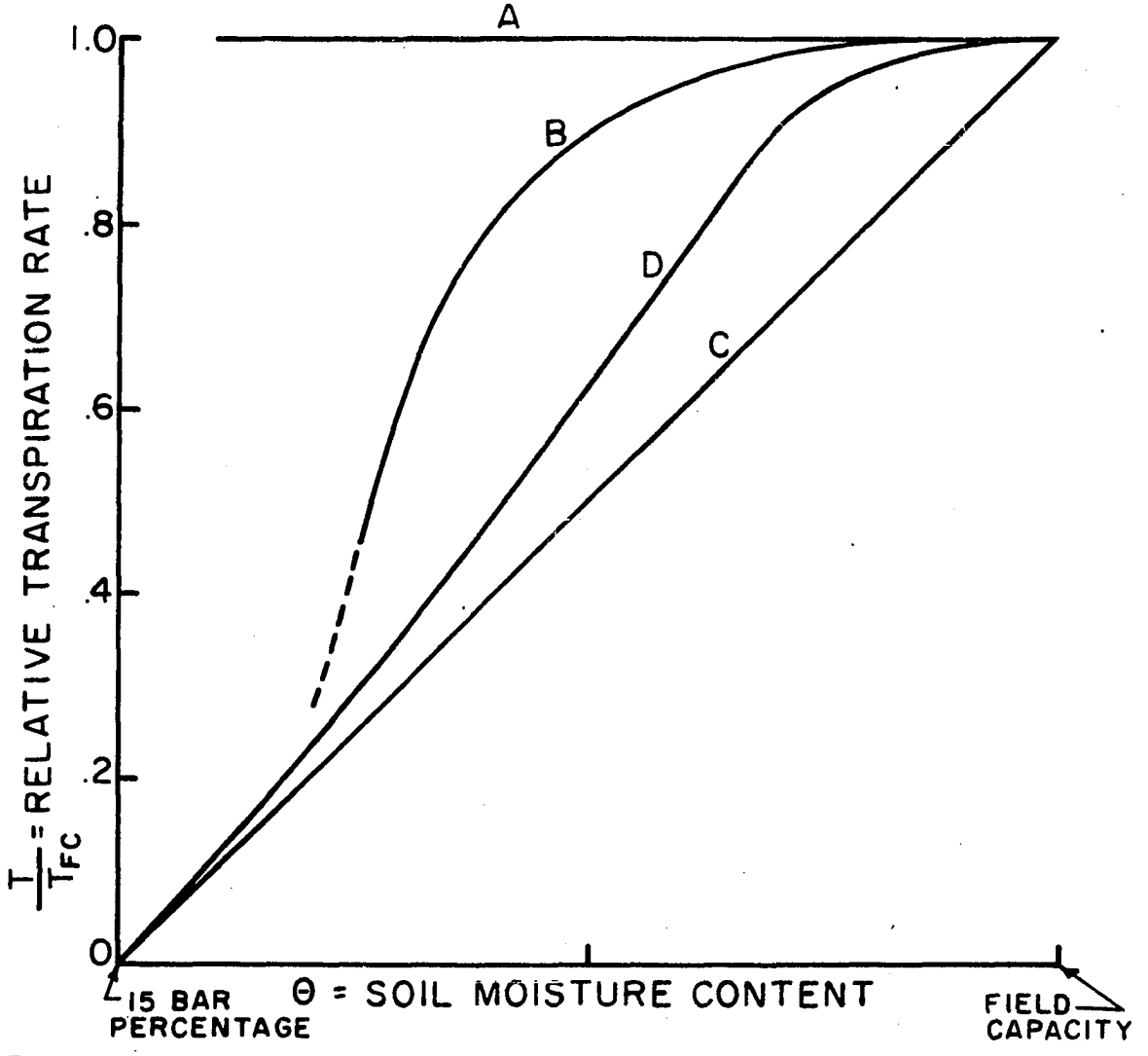


Figure 12. Various proposals for the relationship between relative transpiration rate and soil moisture content. Curve A after Veihmeyer and Hendrickson (1955), curve B after Pierce (1958), curve C after Thornthwaite and Mather (1955), curve D after Halstead (1954)

soil water, curve C, is based on observations taken at O'Neill, Nebraska (Halstead, 1954) in the Great Plains study of 1953. The soil was a sandy loam. The observations were made under very dry atmospheric conditions with moderately high radiation intensities. It is seen that curve C, or better, curve D, which is redrawn from the original O'Neill data, agree closely with a curve obtained for a moderately high potential transpiration rate in the present experiment (see Figure 9 for comparison).

Wilting in Relation to Soil Moisture Content and Meteorological Conditions

Theoretical

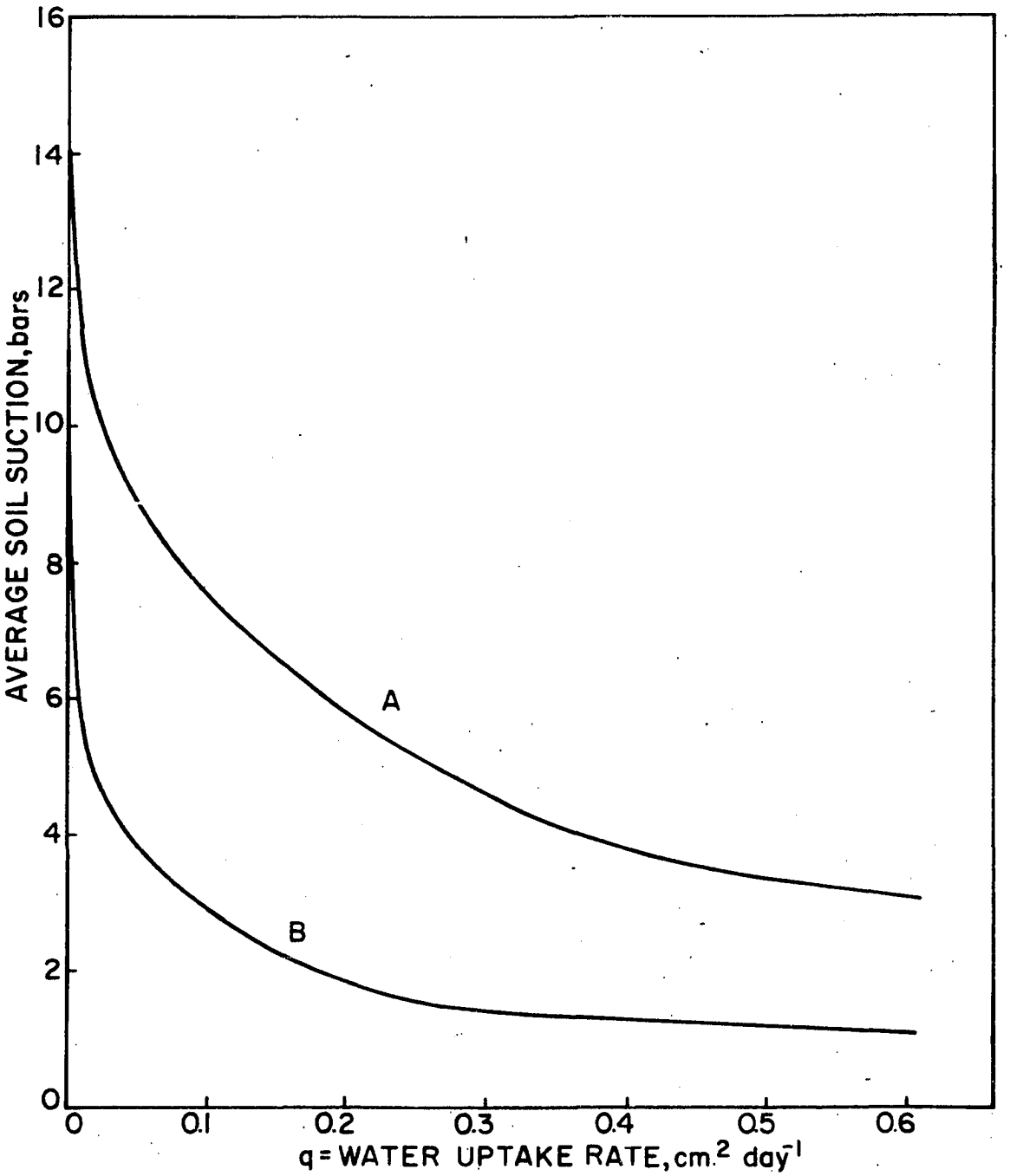
In discussing the wilting point in the introductory section, it was pointed out that the permanent wilting point is the moisture content of the soil at which plants wilt (lose turgor) and do not recover turgor when placed in a saturated atmosphere. Essentially, it is the moisture content at which plants wilt when the potential transpiration rate is negligibly small. Empirically, it is found that for most soils, the permanent wilting point corresponds closely to a soil suction of 15 bars. By the above definition of the permanent wilting point, the soil suction should be approximately 15 bars uniformly throughout the soil; thus, we can consider that plants wilt when the soil suction at the root

surface has attained a value of 15 bars.

Under this assumption, we can examine the wilting point from a dynamic viewpoint via the flow equation by examining the progress in soil suction at the root surface. The wilting point will be the average value of soil suction in the root zone when the soil suction at the root surface has attained a value of 15 bars. The results of such calculations are presented in Figure 13, where the average soil suction in the root zone when the suction at the plant root is 15 bars is shown as a function of the water uptake rate q. Two curves are presented in Figure 13. Curve A was calculated using values of K taken from data of Gardner (1960). Curve B was calculated with K values 1/10 of those used for curve A. It is believed that these values of K will span most of the values commonly found in soil.

At low uptake rates, the average soil suction is close to the suction at the plant root. For high uptake rates, large differences between the two occur. This is because larger gradients of soil suction are required to move water to the root as q (or T) increases. Thus, as potential transpiration rate increases, plants will wilt at higher average soil moisture contents. The curves in Figure 13 indicate that over the range of potential transpiration rates likely to be encountered in the field, the average soil suction at wilting varies from 15 to 1 or 3 bars. At soil suc-

Figure 13. Average soil suction in the root zone when the soil suction at the root surface is 15 bars, as a function of water uptake rate by the roots. Curve A calculated using capillary conductivity data of Gardner (1960). Curve B calculated using capillary conductivity values one-tenth of those used for curve A


16
14
12
10
8
6
4
2
0
AVERAGE SOIL SUCTION, bars
A
B
0
0.1
0.2
0.3
0.4
0.5
0.6
q = WATER UPTAKE RATE, cm.2 day-1

tions lower than 1 to 3 bars, little effect of potential transpiration rate would be encountered.

The calculations represented by Figure 13 are over simplified in that they assume that transpiration proceeds at the potential rate until the suction at the root has attained a value of 15 bars, at which point the whole plant loses turgor and wilts. Changes in transpiration rate due to reduced turgor in the leaves and reduced permeability of the plant with decreased turgor are neglected. The errors involved in these assumptions appear to be of small magnitude at low transpiration rates but they are probably of considerable importance at higher transpiration rates.

Experimental

In the container experiment, the estimate of the wilting point was taken to be the point on the curves depicting actual transpiration rate as a function of soil moisture content, such as those shown in Figure 7, where the actual transpiration rate departed from the constant rate phase, i.e., the point on the curve where T became less than T_{FC}. For example, the values of the wilting point for the three days depicted in Figure 7 are 34.2% on July 30, 28.2% on August 13 and 22.6% on August 5. To distinguish the wilting point referred to in this discussion from the permanent wilting point, the wilting point is here referred to as the

turgor loss point θ_{TL}, with the subscript TL referring to turgor loss. If the permanent wilting point corresponds to a soil suction of 15 bars at the root, then it is true that plants will wilt permanently when the average soil moisture content is at a value of θ_{TL}, if the current transpiration conditions are maintained. However, if the potential transpiration rate is lessened, as it is at night, and as it is in the day when net radiation is reduced or when the water vapor content of the atmosphere is increased, the plant will recover turgor.

Since the values of the turgor loss point obtained in the container experiment are estimates of the true values, they have been designated as estimated turgor loss points θ^*_{TL}. The value of θ^*_{TL} represents the value of θ when the effects of reduced turgor on the transpiration rate were becoming evident. This value will over-estimate the true θ_{TL} by a small amount, but since a small decrease in the average soil moisture content at this point results in a very large increase in the soil suction at the root surface, it is felt that θ^*_{TL} is probably within 2 or 3% by volume of the true value of θ_{TL}.

The relationship between θ^*_{TL} and the transpiration rate at field capacity T_{FC} is shown in Figure 14. It is seen that at low values of T_{FC}, θ^*_{TL} approaches the 15-bar percentage of 22%, while at high values of T_{FC}, θ^*_{TL} approaches a value

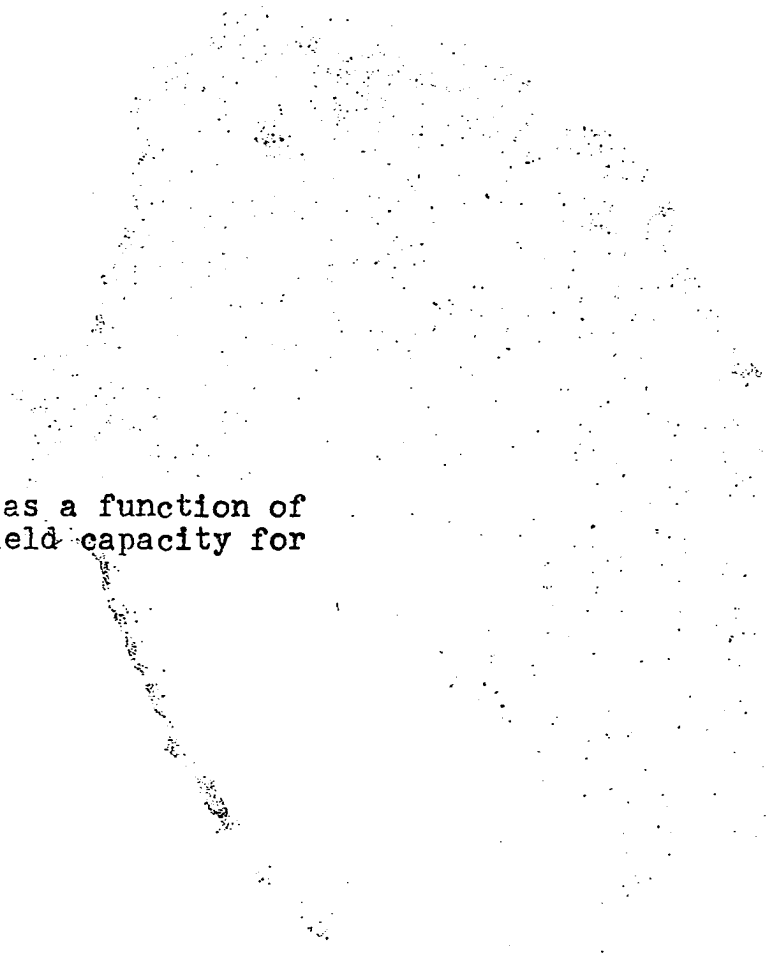
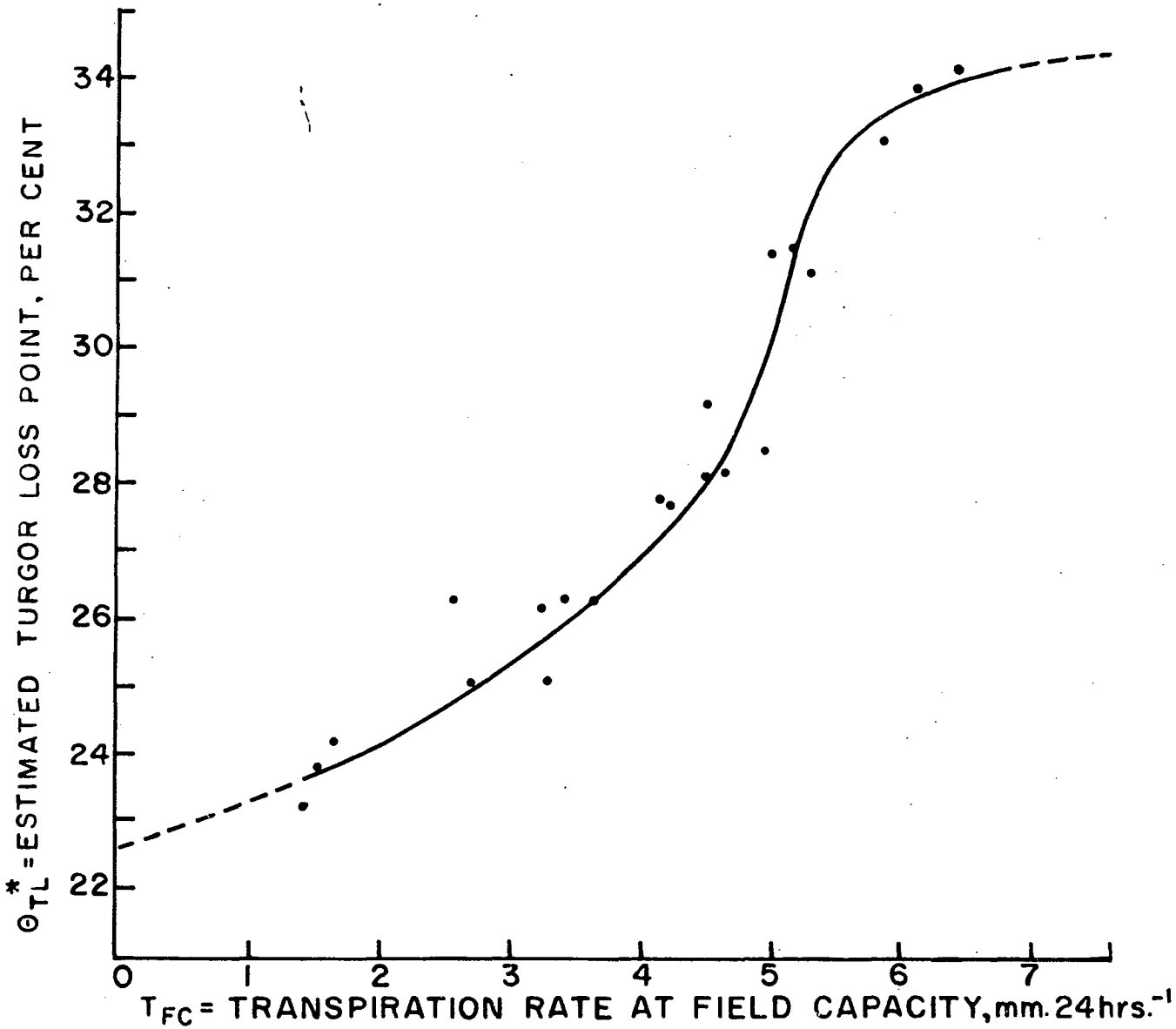


Figure 14. Estimated turgor loss point as a function of the transpiration rate at field capacity for Colo silty clay loam

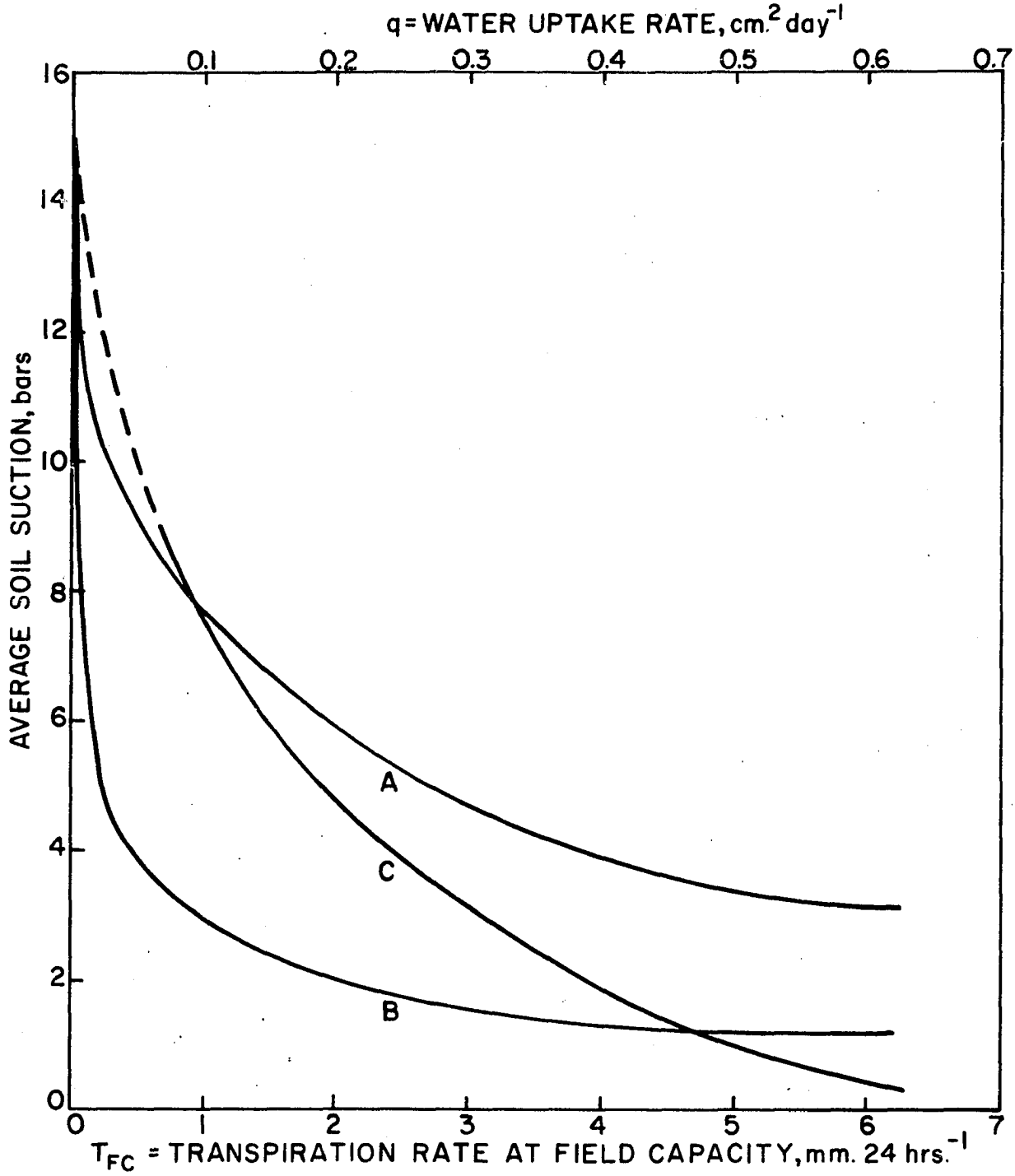

θ_{TL}^* = ESTIMATED TURGOR LOSS POINT, PER CENT
34
32
30
28
26
24
22
0
1
2
3
4
5
6
7
T_{FC} = TRANSPIRATION RATE AT FIELD CAPACITY, mm. 24hrs.$^{-1}$

of 34%, not much less than the field capacity, 36%.

The values of θ^*_{TL} agree quite well with field observations of the incidence of wilting taken during the course of the experiment. Observations on many days confirmed the fact that plants growing at soil moisture contents greater than θ^*_{TL} appeared to be maintaining full turgor, while plants growing at soil moisture contents less than θ^*_{TL} showed greyish discoloration with some curling, particularly in the top leaves. It was also observed that, whereas on days when the value of T_{FC} was high, plants growing at soil moisture contents less than θ^*_{TL} were wilting, the same plants on a succeeding day with a lower value of T_{FC} would show no sign of wilting as long as θ was greater than θ^*_{TL}.

The curve plotted in Figure 14 is replotted in Figure 15 to show the soil suction corresponding to θ^*_{TL}, as a function of T_{FC}. For comparison, the calculated curves shown in Figure 13 are also shown in Figure 15. Considering the assumptions involved, there is reasonable agreement between the theoretical relationship and the observed relationship. There is some discrepancy at the higher transpiration rates. It is believed that this discrepancy probably arises from an appreciable decrease in permeability of the plant at high transpiration rates.

Figure 15. Soil suction corresponding to the estimated turgor loss point, as a function of the transpiration rate at field capacity for Colo silty clay loam, curve C. Curves A and B as in Figure 13


q = WATER UPTAKE RATE, cm.^{2} day^{-1}
0.1
0.2
0.3
0.4
0.5
0.6
0.7
AVERAGE SOIL SUCTION, bars
16
14
12
10
8
6
4
2
0
A
C
B
0
1
2
3
4
5
6
7
T_{FC} = TRANSPIRATION RATE AT FIELD CAPACITY, mm. 24 hrs.$^{-1}$

Wilting and Plant Growth

Production of dry matter

Since photosynthesis is dependent on diffusion of carbon dioxide through the stomata, and since the stomata close when turgor in the leaf is lost, it is to be expected that, when a plant wilts and loses turgor, photosynthesis will cease. (Most of the available literature, e.g., de Wit (1958), indicates that partial closure of the stomata has little effect on CO_2 diffusion until the stomata are almost completely closed.) Consequently, one would expect that the production of dry matter by a plant growing under conditions where soil water supply is limiting would be rather closely related to the incidence of wilting. The measurements of dry matter accumulation made in section 1 of the container experiment were used to investigate the effects of wilting on the production of dry matter.

The total number of days on which θ was less than θ_{TL}^{*} was determined for each treatment along with the reduction in dry weight below that of the control plants. In this way, the relationship between wilting and plant production of dry matter could be followed. The days on which θ was less than θ_{TL}^{*} were not necessarily successive days. In some instances, because of frontal passages and consequent changing weather patterns, potential transpiration rate would

decrease from one day to the next with a corresponding decrease in the value of θ_{TL}. Thus, θ was sometimes less than θ^*_{TL} on one day and greater than θ^*_{TL} on the following day or, in some cases, on the following two days. The relationship between the reduction in dry weight accumulation and the number of days on which θ was less than θ^*_{TL} is shown in Figure 16. Each plotted point is the mean for the four replicates subjected to the same soil moisture treatment.

The fitted regression line in Figure 16 is linear and passes close to the origin; the intercept is not significantly different from zero. The slope of the regression line, 14.5 g. per hill of corn per day is close to the mean growth rate of the control plants during the experiment, viz., 13.9 g. per hill of corn per day. On this evidence, θ^*_{TL} does seem to have the significance claimed for it. Once θ is less than θ^*_{TL}, the plant virtually ceases to assimilate.

In examining the relationship of dry matter accumulation to the incidence of wilting, it has been tacitly assumed that the control plants were gaining weight at a constant rate throughout the experiment. That this is an oversimplification is seen by reference to Figure 17, in which the rate of dry matter accumulation by the control plants is shown. The rate of increase in leaf area is also shown in Figure 17. The standard errors of the mean dry weight determinations are shown at each sampling period. As is to be expected in an

Figure 16. Reduction in dry weight of plants subjected to various periods of soil moisture stress as a function of the number of days in the stress period on which soil moisture content was less than the estimated turgor loss point

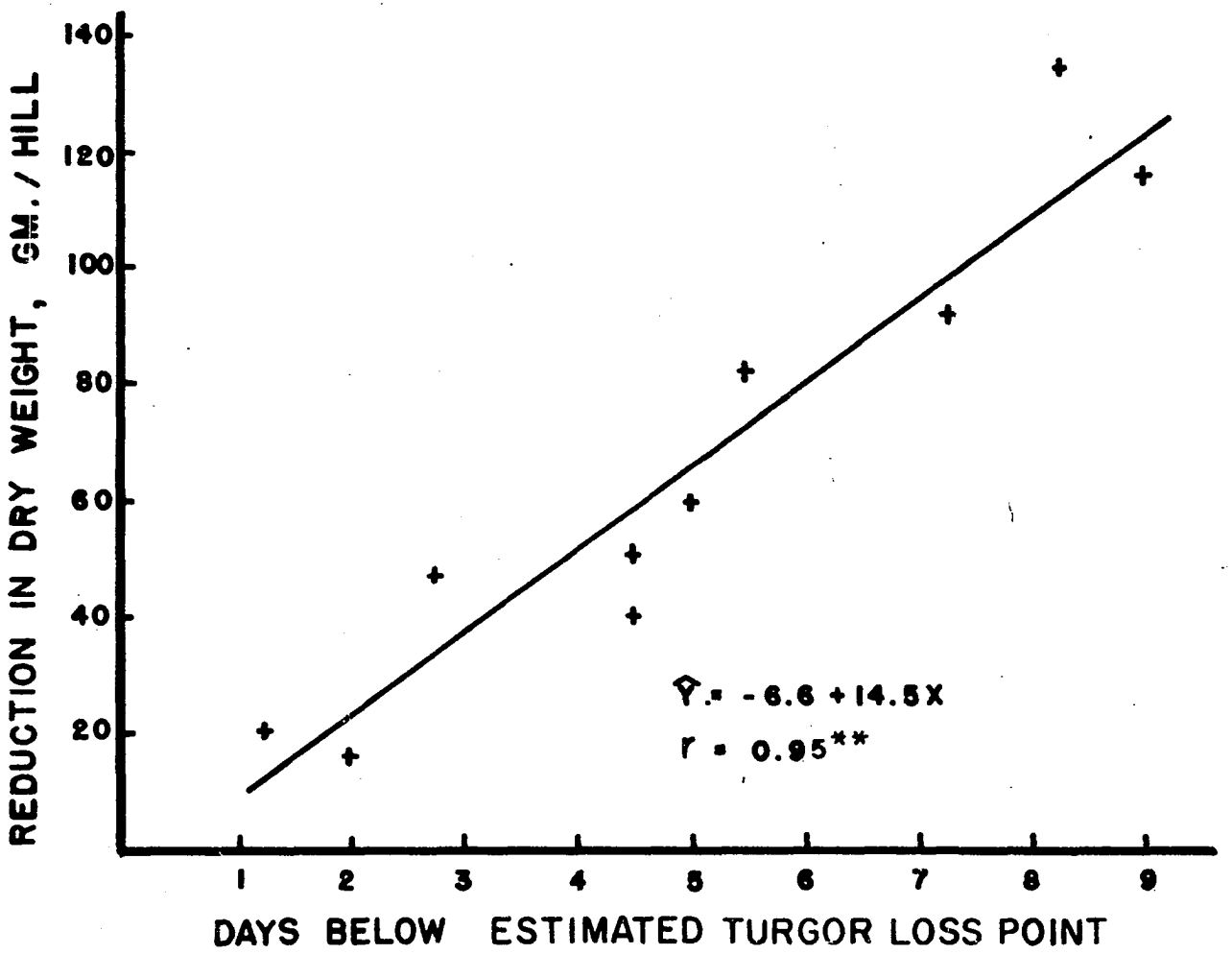
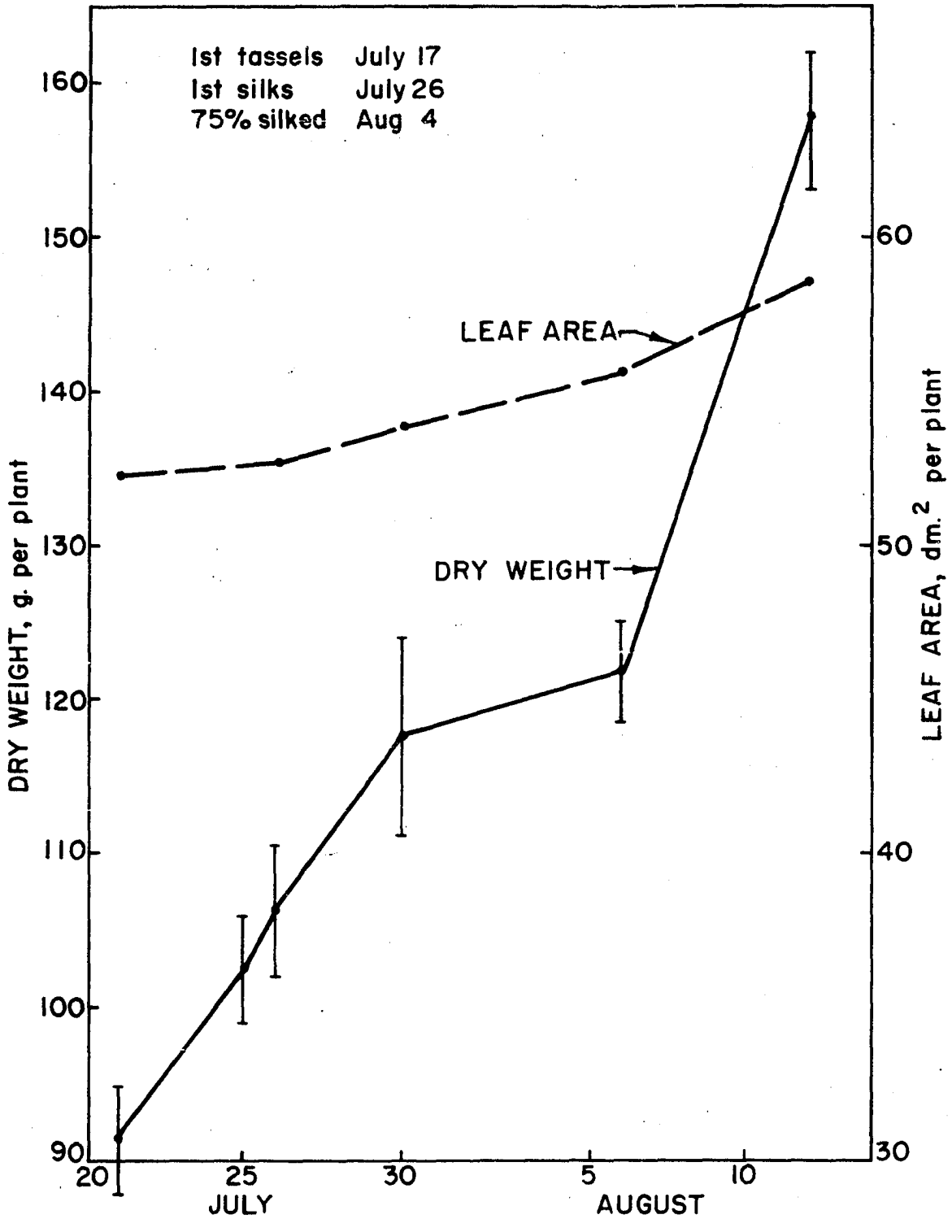

REDUCTION IN DRY WEIGHT, GM. / HILL
140
120
100
80
60
40
20
1
2
3
4
5
6
7
8
9
DAYS BELOW ESTIMATED TURGOR LOSS POINT
Ŷ = -6.6 + 14.5X
r = 0.95**

Figure 17. Cumulative dry weight and cumulative leaf area of control plants. The vertical lines about the dry weight points represent the standard errors of the dry weight determinations


1st tassels July 17
1st silks July 26
75% silked Aug 4
LEAF AREA
DRY WEIGHT
DRY WEIGHT, g. per plant
LEAF AREA, dm.2 per plant
160
150
140
130
120
110
100
90
60
50
40
30
20
25
30
5
10
JULY
AUGUST

experiment of this type in which the sample is small and the time intervals involved are also rather small, the standard errors are rather high. It is evident from the figure that the assumption of a constant growth rate was a fairly reasonable one, except for the first week in August, a cloudy, wet period in which growth rates were considerably reduced. When the soil suction was allowed to attain values of 5 and 15 bars, the number of days on which θ was less than θ^*_{TL} was generally between 5 and 9 so that small daily fluctuations in growth rate would introduce only small errors in the assumption of a constant growth rate, provided that none of the stress periods coincided closely with the first week in August. This latter was the case, except for one treatment in which soil suction was allowed to attain a value of 5 bars at about August 3, and one treatment in which soil suction was allowed to attain a value of 15 bars at about August 7. When the suction was allowed to attain a value of 2.5 bars, the number of days on which θ was less than θ^*_{TL} was between 1 and 3 so that a somewhat larger error in the assumption of a constant growth rate was possible. Only one of these treatments coincided with the first week in August, viz., one treatment in which soil suction attained the value of 2.5 bars at about August 2.

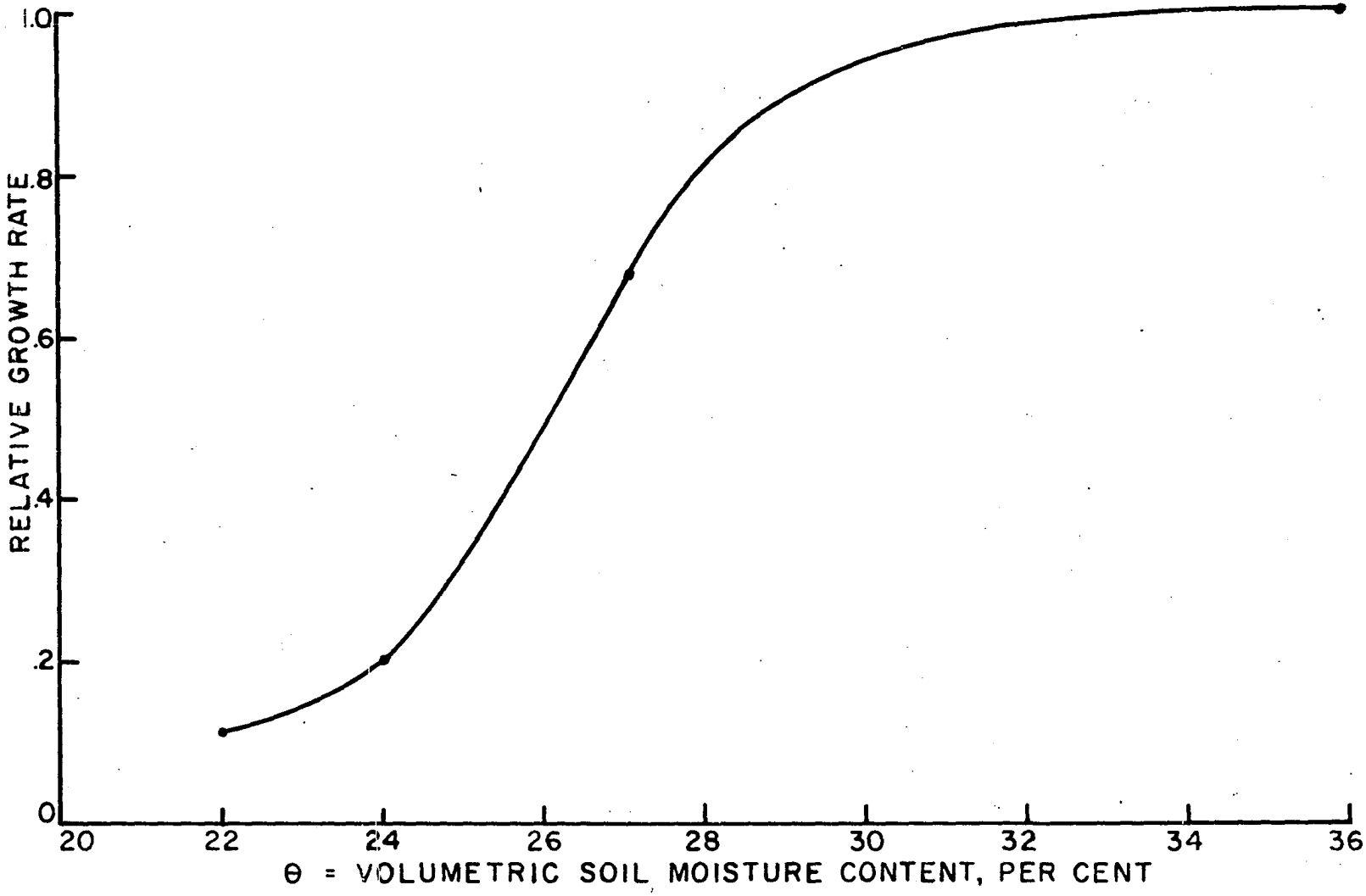
In humid regions, one encounters a constantly changing environment in which the potential transpiration rate

fluctuates. Consequently, θ_{TL} will fluctuate almost from day to day. An idea of the average effects on dry matter accumulation that might be encountered in the field under these conditions can be obtained by reference to Figure 18 in which the average relative growth rate (increase in dry weight/increase in dry weight of control plants over the same period) for the several soil moisture treatments imposed under the fluctuating weather conditions pertaining during the course of the container experiment is shown. The points shown in the figure are the means of the 3 soil moisture treatments imposed. The relation between relative growth rate and soil moisture content is similar to the relation between relative transpiration rate and soil moisture content under moderate transpiration conditions (see Figure 9 for comparison).

Grain yield

The prediction of the effects of soil moisture stress on plant response is complicated by the fact that various aspects of the plant's functioning and growth are not affected uniformly by soil moisture stress. For example, Hagan et al. (1957) found that dry weight production of vegetative material, photosynthesis and respiration rates of ladino clover were not affected appreciably until the moisture content in the entire root zone approached the 15-bar per-

Figure 18. Relative growth rate of plants subjected to soil moisture stress (increase in dry weight/increase in dry weight of control plants over the same period) as a function of soil moisture content


1.0
.8
.6
.4
.2
0
RELATIVE GROWTH RATE
20
22
24
26
28
30
32
34
36
θ = VOLUMETRIC SOIL MOISTURE CONTENT, PER CENT

centage, while green weight production and shoot elongation were reduced significantly when the soil moisture content fell below a value corresponding to 1 bar suction. With corn, as with most agricultural crops which are grown for grain production, the effects on grain yield depend on the time in the growing season at which soil moisture stress occurs. Denmead and Shaw (1960), for example, showed that stress occurring before tasseling could reduce grain yields appreciably. The effect was indirect. The primary action seemed to be a reduction in the rate of leaf area expansion so that, at the time when the ear was filling, there was less leaf area available for photosynthesis and consequent accumulation of dry matter in the grain. Stress imposed during silking had a double effect. Ear development and fertilization appeared to be adversely affected so that less grain developed on the cobs. At the same time, through reducing photosynthesis, wilting reduced the accumulation of dry matter in the grain. Stress imposed after the silking period appeared to have a direct effect through reducing assimilation at a time when most of the assimilate was being used in grain production. Considering all periods, grain yield was most severely affected by the occurrence of soil moisture stress during the silking period.

Section 2 of the present experiment was designed to indicate the time at which corn is most sensitive to moisture

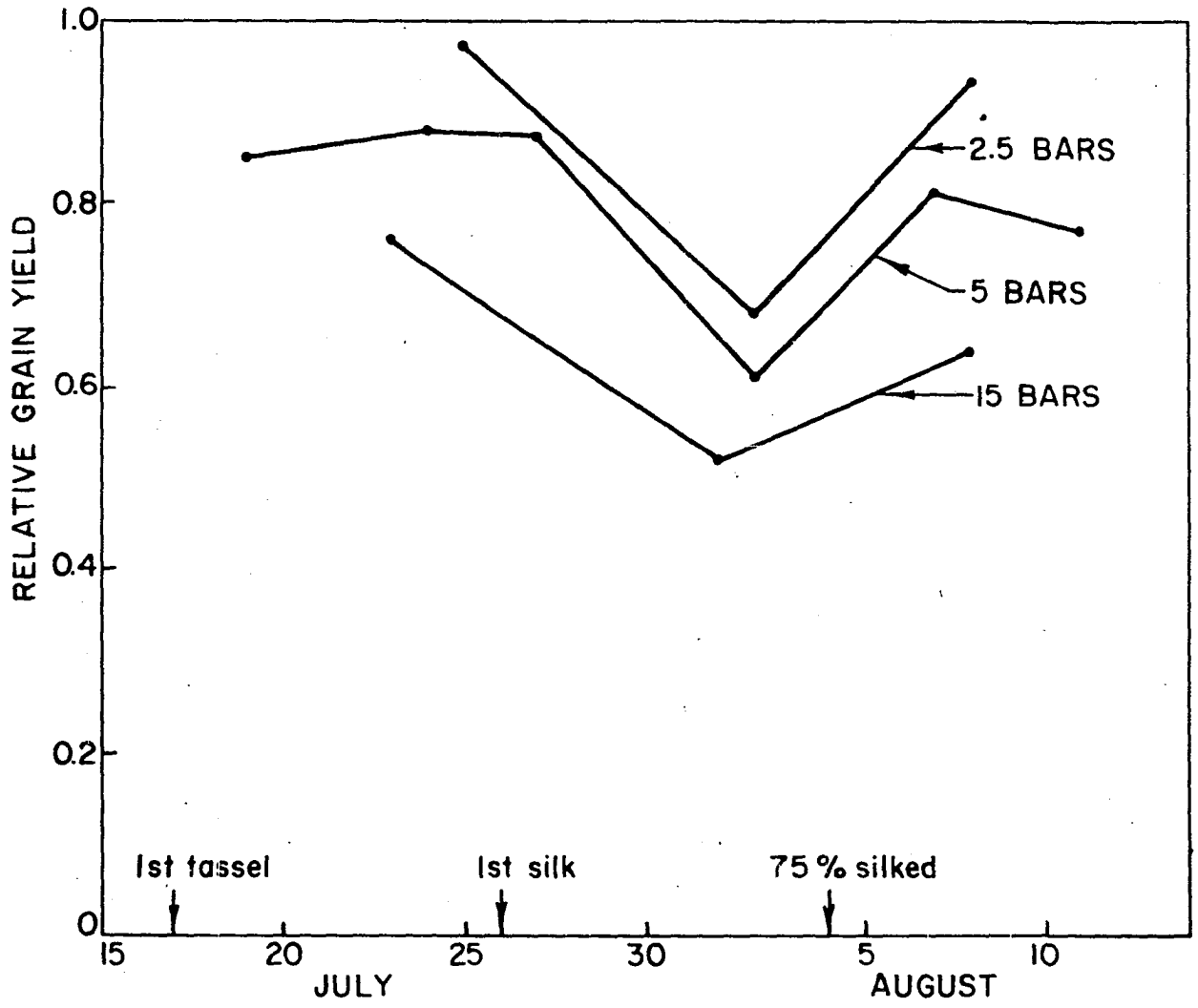
stress during the critical silking period. The effects of soil moisture stress on relative grain yield of the control plants, are shown in Figure 19. The points plotted in the figure represent the relative grain yields of plants growing in soil in which the soil suction was allowed to increase to values of 2.5, 5 and 15 bars respectively at the times shown in the design of the experiment in Table 2. The points are the means of the four replicates; they are plotted at the mid-points of the time interval necessary for the increase of the soil suction to the desired value.

The data in Figure 19 indicate that grain yield is most affected by soil moisture stress occurring at about the 50% silking date. Soil moisture stress occurring prior to silking appears to have the least effect on grain yield. Soil moisture stress occurring after silking appears to reduce grain yields somewhat more than stress before silking, but the effect is not as great as stress occurring during the silking period itself.

Transpiration and Net Assimilation Rate

Many experiments with individual leaves and single plants, e.g. Verduin and Loomis (1944), Chapman and Loomis (1953), Böhnig and Burnside (1956), Ashton (1956), have shown that, below radiation intensities of 0.2 to 0.4 cal. $cm.^{-2}$ $min.^{-1}$, the assimilation of carbon dioxide by the leaves is

Figure 19. Relative grain yield of plants subjected to soil moisture stress (grain yield/grain yield of control plants) at different pericds during the growing season. The values of soil suction shown in the figure, fiz. 2.5 bars, 5 bars and 15 bars, refer to the soil suction developed in the root zone before the plants were irrigated


1.0
0.8
0.6
0.4
0.2
0
RELATIVE GRAIN YIELD
2.5 BARS
5 BARS
15 BARS
1st tassel
1st silk
75 % silked
15
20
25
30
5
10
JULY
AUGUST

strongly dependent on light intensity, while, at radiation intensities greater than these values, assimilation is no longer light dependent. On the other hand, with field crops, where there is much mutual shading of leaves, assimilation of carbon dioxide appears to increase with increasing light up to the radiation intensities of full sunlight (1.2 to 1.6 cal. $cm.^{-2}$ $min.^{-1}$). This is apparent from the work of Thomas and Hill (1950), Moss (1959) and Denmead (1961).

In Figure 20, the NAR of the control plants in section 1 of the experiment and the transpiration rate at field capacity have been plotted as functions of time for the duration of the experiment, along with the values of net radiation measured over adjoining field grown corn at the experimental site and the daily maximum temperature. The values of NAR are plotted at the mid-points of the sampling intervals over which they were determined. The values of transpiration rate, net radiation and daily maximum temperature are averages for periods of 4-5 days and are plotted at the mid-points of the periods. Both NAR and transpiration rate appear to be closely related to the net radiation. They also appear to be closely related to the daily maximum temperature, but it is believed that these latter relationships are of an associative rather than a causative nature. With increasing intensity of insolation,

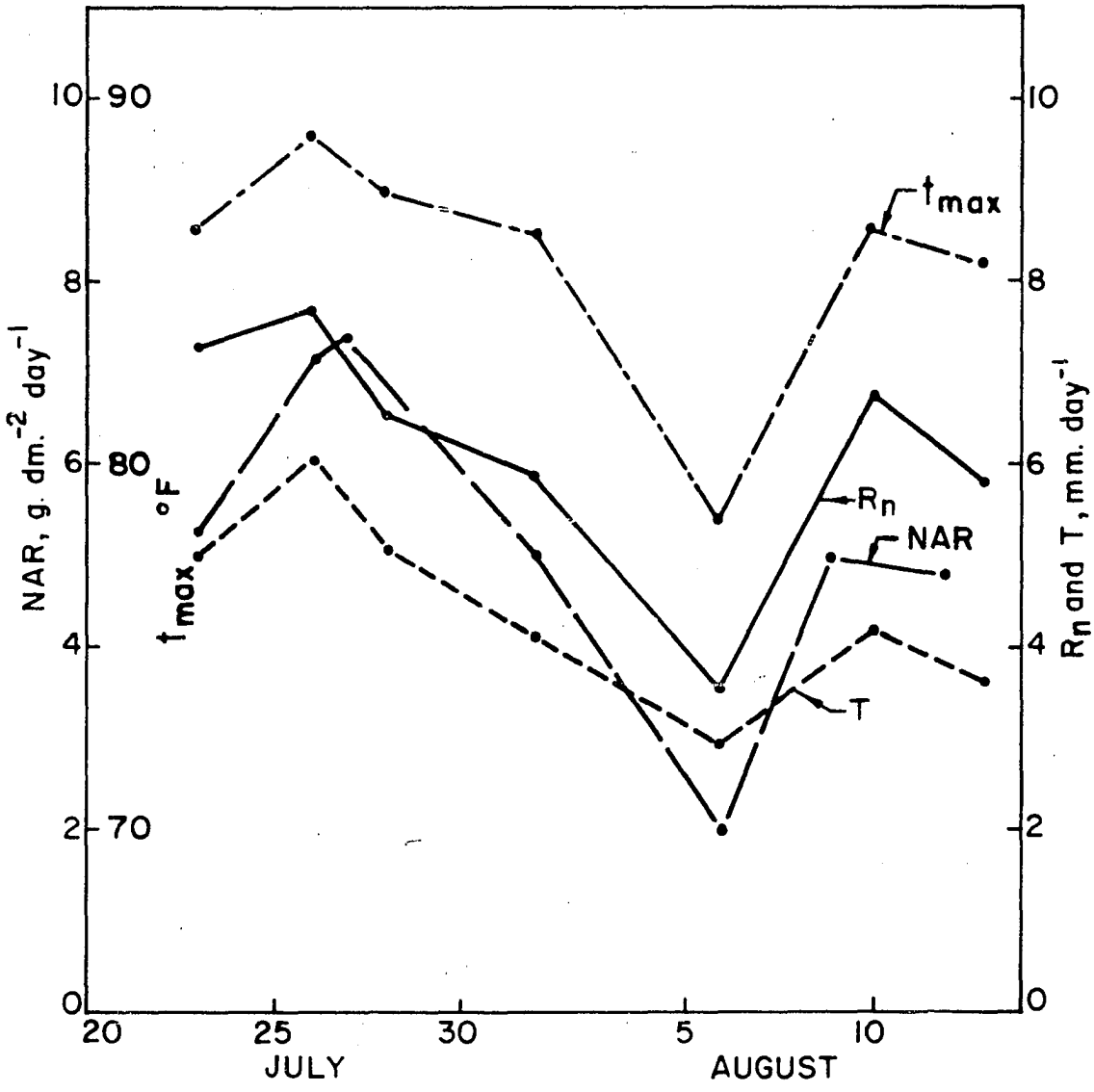
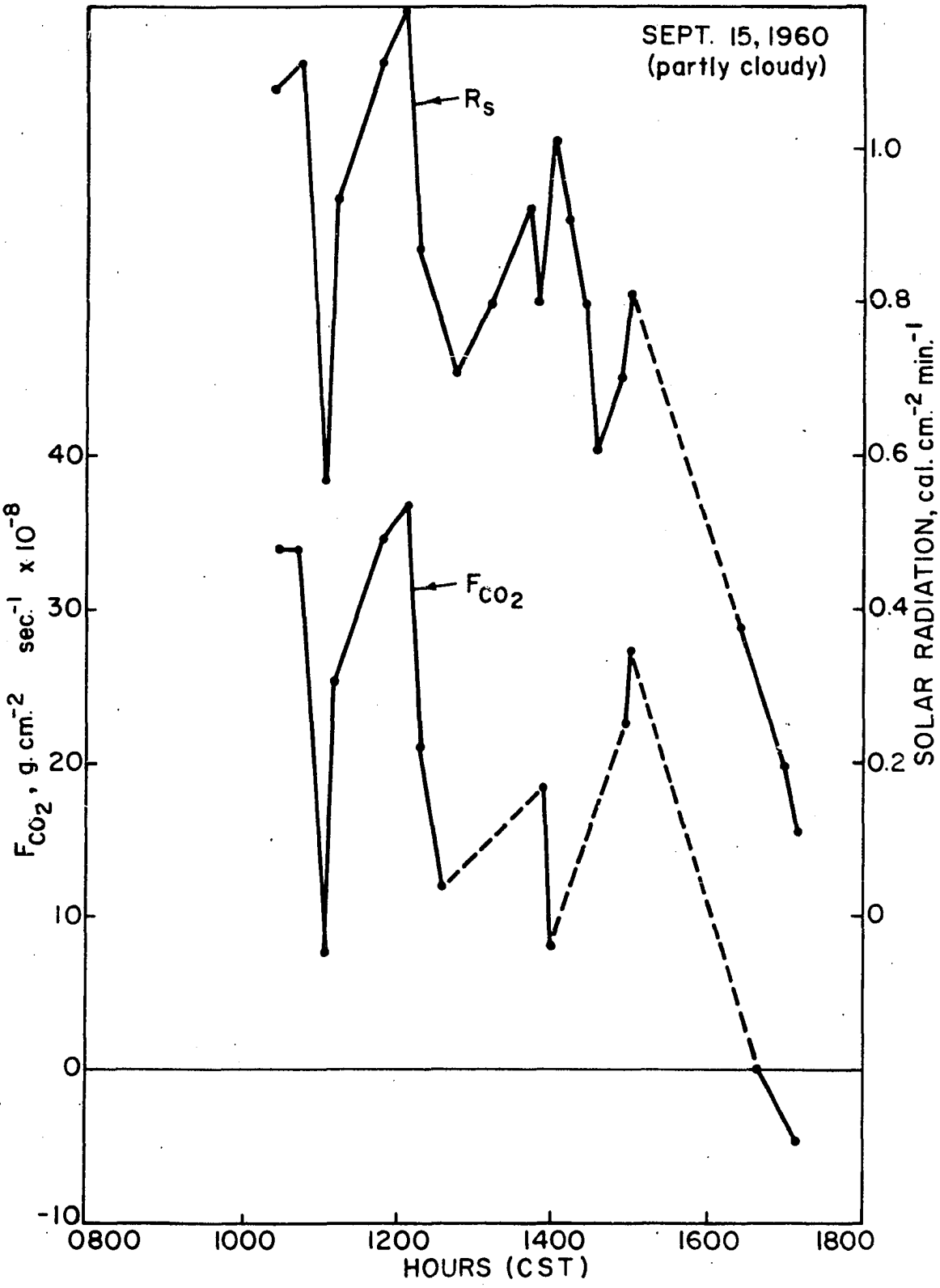


Figure 20. Net assimilation rate NAR, average transpiration T, average net radiation R_n, and average daily maximum temperature t_{max} for different periods throughout the experiment

there is increasing assimilation and transpiration, and, as a parallel effect of the same cause, there is increasing heat transfer to the air with a consequent increase in temperature.

NAR does appear to be more sensitive to variation in net radiation intensity than transpiration, i.e., a given percentage change in net radiation appears to be associated with a relatively large percentage change in NAR compared to the associated percentage change in transpiration. This difference can be explained by a closer examination of the relationships between NAR and radiation intensity, and transpiration and radiation intensity. Figure 21 presents some data obtained by Denmead (1961) in measurements of the turbulent transfer of carbon dioxide between the atmosphere and an actively growing corn crop, well supplied with soil water. The flux of carbon dioxide, F_{CO_2}, expressed in grams CO_2 exchanged per square centimeter of leaf surface per second, and the solar radiation intensity, R_s, expressed as calories received on one square centimeter of a horizontal surface per minute, are shown for different times of the day. The flux of carbon dioxide was estimated by the aerodynamic technique described in the introductory section, which required simultaneous measurements of the vertical profiles of horizontal wind

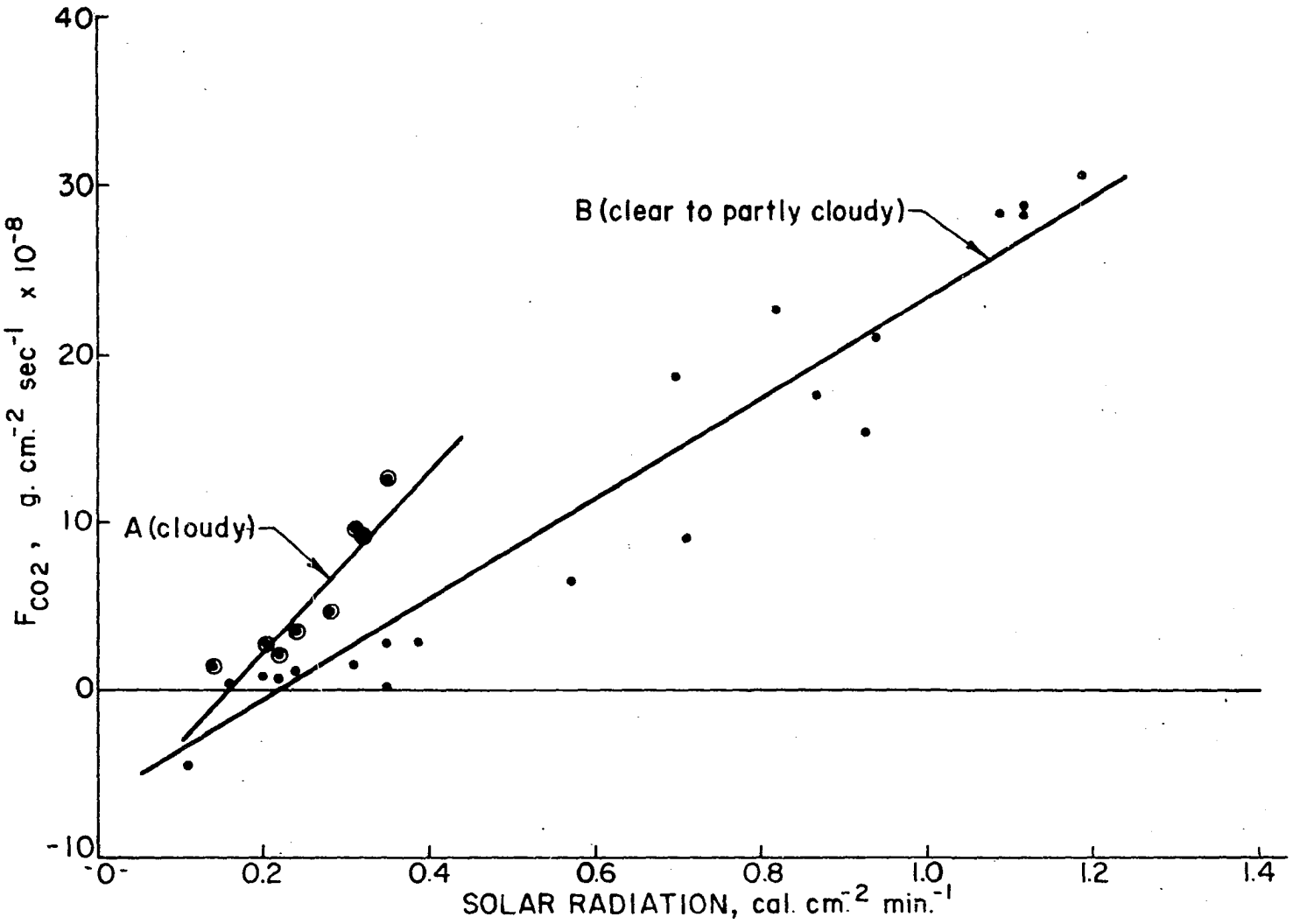
Figure 21. Diurnal variation in the flux of carbon dioxide between the atmosphere and a corn crop F_{CO_2} and in solar radiation R_s at Ames, Iowa on September 15, 1960 (after Denmead, 1961)


SEPT. 15, 1960
(partly cloudy)
R_s
F_{CO_2}
F_{CO_2}, g.cm.$^{-2}$ sec.$^{-1}$ x 10^{-8}
SOLAR RADIATION, cal. cm.$^{-2}$ min.$^{-1}$
40
30
20
10
0
-10
1.0
0.8
0.6
0.4
0.2
0
0800
1000
1200
1400
1600
1800
HOURS (CST)

velocity and carbon dioxide concentration. The measurements were obtained in runs of 5 minutes duration made at the various times of the day. Solar radiation was measured with an Eppley pyrheliometer located on top of the Agronomy building, about 1/2 mile distant from the experimental site. The day represented in Figure 21, September 15, 1960, was partly cloudy with intermittent sun and shade. The flux of carbon dioxide appears to be very sensitive to fluctuations in radiation intensity.

The relationship between the flux of carbon dioxide and solar radiation is shown in Figure 22. Curve A shows the relationship observed on a cloudy day, September 14, 1960, while curve B shows the relationship observed on two clear to partly cloudy days, September 13 and 15, 1960. There appear to be somewhat different relationships pertaining on the two types of day. It is believed that this difference arises from a difference in the character of the incoming radiation. On cloudy days, the incoming radiation is primarily diffuse; diffuse radiation is omnidirectional in origin and is more evenly distributed over the upper and lower leaves of the canopy. On clear and partly cloudy days, incoming radiation is primarily direct so that the top leaves of the canopy receive intense radiation while the lower leaves are in shade. In both cases, the compensation point, i.e., the radiation intensity at which photosynthesis balances

Figure 22. Relationship between the flux of carbon dioxide between the atmosphere and a corn crop F_{CO_2} and the intensity of solar radiation R_s (after Denmead, 1961)


40
30
20
10
0
-10
F_{CO2}, g. cm.$^{-2}$ sec^{-1} x 10^{-8}
B (clear to partly cloudy)
A (cloudy)
0
0.2
0.4
0.6
0.8
1.0
1.2
1.4
SOLAR RADIATION, cal. cm.$^{-2}$ min.$^{-1}$

respiration and the net flux of carbon dioxide is zero, appears to be in the vicinity of 0.2 cal. $cm.^{-2}$ $min.^{-1}$. Due to the negative intercept on the y-axis, a certain percentage change in radiation intensity produces a much larger percentage change in the flux of carbon dioxide.

The relationship between the transpiration rate at field capacity measured in the container experiment and net radiation intensity is shown in Figure 23. Transpiration rate is almost directly proportional to net radiation, so that a certain percentage change in radiation intensity produces an almost equal percentage change in transpiration rate.

Returning to Figure 20, it does appear that under the conditions for potential transpiration, i.e., when soil water supply is not limiting transpiration, when soil fertility is not limiting growth and when the plant cover is reasonably complete, a general relationship between the production of dry matter of a crop and its water use should exist. If soil fertility is limiting plant growth, the NAR of the crop will vary, depending on the availability of soil nutrients. If the plant cover is incomplete, the water use will include a variable fraction due to direct evaporation from the soil surface. The magnitude of this fraction will vary, depending on the frequency with which the soil surface is wet or dry.

Provided that soil fertility is not limiting plant growth and that the plant cover is reasonably complete, the simi-

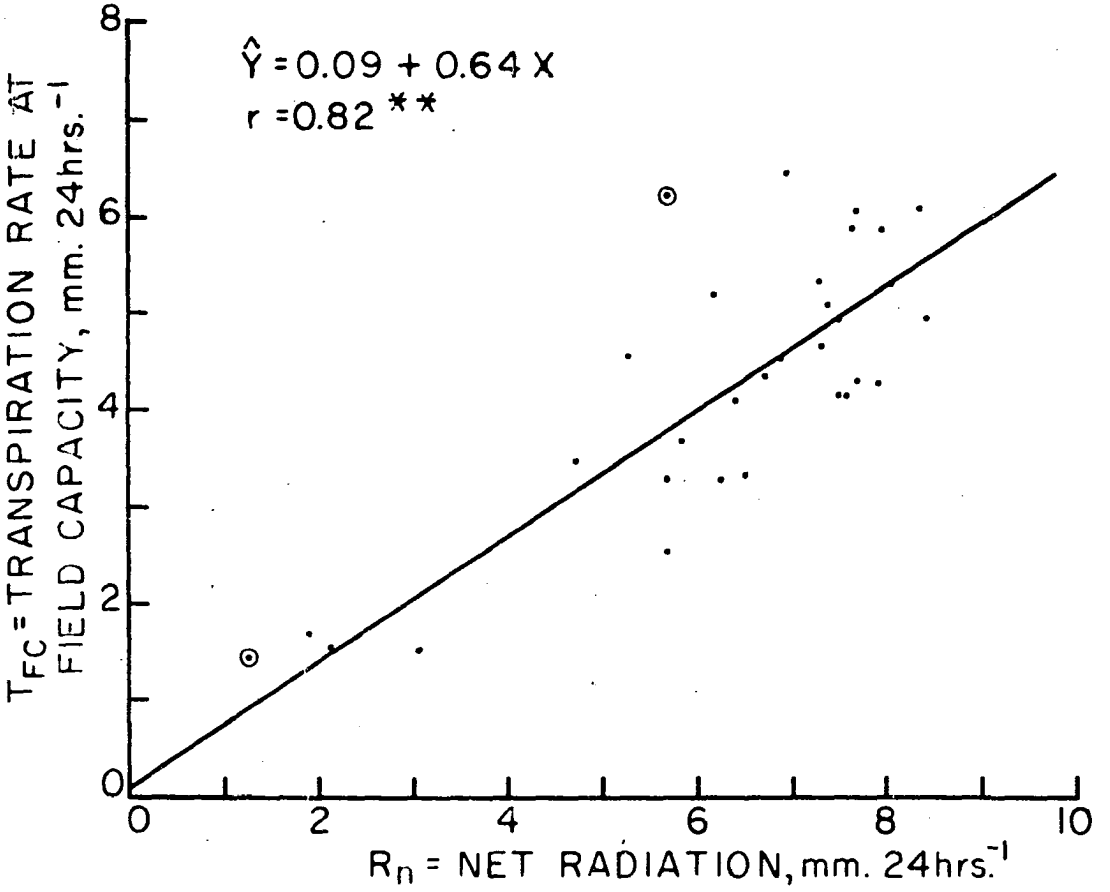


Figure 23. Relationship between daily transpiration rate at field capacity and daily net radiation

larity of the curves relating relative growth rate and soil water content, Figure 18, and relative transpiration rate and soil water content, Figure 9, suggests that the production of dry matter may still be rather closely related to the transpiration rate as soil water supply decreases. Thus, under certain limiting conditions, viz., adequate soil fertility and a reasonably complete crop cover, the concept of the transpiration ratio, which is the ratio of the water use during the growth of a crop to the production of dry matter, may have some useful application. Considerations similar to these have been used to good effect by de Wit (1958) to explain the results of many container and field experiments concerned with the relation between transpiration and crop yields.

When one is dealing with grain yields rather than with the production of dry matter, the situation is more complicated. As is evident in Figure 19, the magnitude of the reduction in grain yield resulting from soil moisture stress depends on the time in the growing season at which the stress occurs. Allowance would have to be made for this phenomenon in developing a general relationship between transpiration and grain yield.

Transpiration Rate in Relation to Meteorological Conditions

The dependence of transpiration rate on meteorological conditions when water is readily available to the plant has been mentioned several times in previous sections of this thesis. The data in Figure 23 indicate the dependence of transpiration on net radiation. Of the weather factors that influence evaporation, net radiation is by far the most important. This is evident when one compares Figure 23 with Figure 24 which shows the relationship between transpiration rate and the evaporation of an open water surface computed by the method of Penman (1956). Penman's equation is

$$E_o = \frac{\Delta R_n + \gamma E_a}{\Delta + \gamma}$$

where E_o is the evaporation of an open water surface in mm., Δ is the slope of the saturation vapor pressure vs. temperature curve at the air temperature in mm. Hg $^{\circ}C^{-1}$, γ is a constant in Bowen's ratio = 0.49 mm. Hg $^{\circ}C^{-1}$, R_n is the net radiation in units of equivalent evaporation of water, i.e. in mm., and E_a is given by the relationship

$$E_a = 0.35(e_s - e_a)(0.5 + u/100)$$

where e_s is the saturation vapor pressure at the air temperature in mm. Hg, e_a is the actual vapor pressure of the air in mm. Hg, and u is the wind velocity in miles per day. The

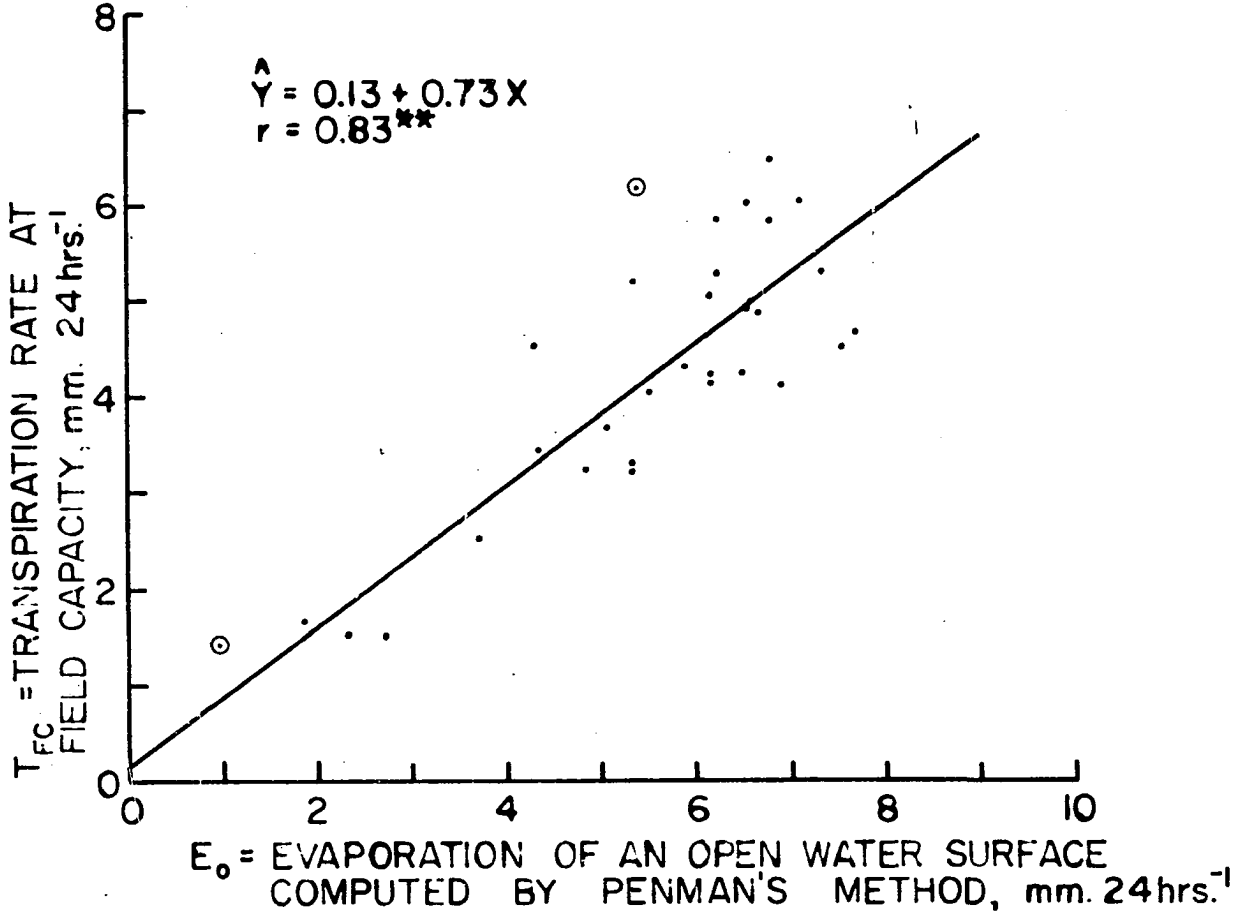


Figure 24. Relationship between daily transpiration rate at field capacity and the estimated evaporation of an open water surface computed by the method of Penman (1956)

equation attempts to partition the net radiation into the energy used in evaporation and the energy used for heating the air. To do this, it takes account of factors additional to the net radiation, viz., vapor pressure and wind velocity.

The points represented by ringed dots in Figures 23 and 24 were obtained on days on which it was felt that advection of heat may have occurred, (T_{FC} was greater than R_n). These points were excluded in computing the regression equations shown in the bodies of the figures. A visual comparison of the two figures would suggest that little is gained by taking account of the factors additional to net radiation, and this is confirmed by comparing the respective correlation coefficients, which differ by only 0.01. It is believed that most of the variation of the points about the regression lines in the figures results from errors involved in determining the transpiration rates, rather than from inadequacies in the physical theory of evaporation.

Penman's potential transpiration rate is estimated from the computed evaporation of an open water surface, E_o, by multiplying E_o by a crop factor. The crop factor varies with the season of the year and is a function of the daylength and the resistance to diffusion of water vapor up through the stomata to the free atmosphere. According to Penman, the factor varies from 0.6 to 0.8 with an average yearly value of 0.75. Scholte Ubing (1959) has shown that the factor

also varies with net radiation. He attributes this variation to changes in the various plant and weather factors which operate to control transpiration under different weather conditions. At low radiation intensities, partial stomatal closure may reduce transpiration in relation to open water evaporation, whereas, at high radiation intensities, this limitation is not present. Scholte Ubing also suggested that variations in turbulent and convective heat and vapor transport under different radiation conditions could introduce error into the calculation of E_o.

This variation in the crop factor was observed in the container experiment. Figure 25 shows the variation in the ratio T_{FC}/E_o with variation in T_{FC}. The ratio varied from a mean value of 0.6 to a mean value of 0.95 as T_{FC} increased from 1 to 6 mm. 24 hrs.$^{-1}$. Despite this complication, the value of the regression coefficient in the relationship between T_{FC} and E_o, shown in Figure 23, was 0.73. This agrees quite well with Penman's average value of 0.75 and we can say that, for practical purposes, the value of T_{FC} measured in the container experiment was equal to the potential transpiration rate.

Since the transpiration rate from plants well supplied with soil water is primarily determined by meteorological conditions, in particular by net radiation, one would expect that, for any given set of meteorological conditions, po-

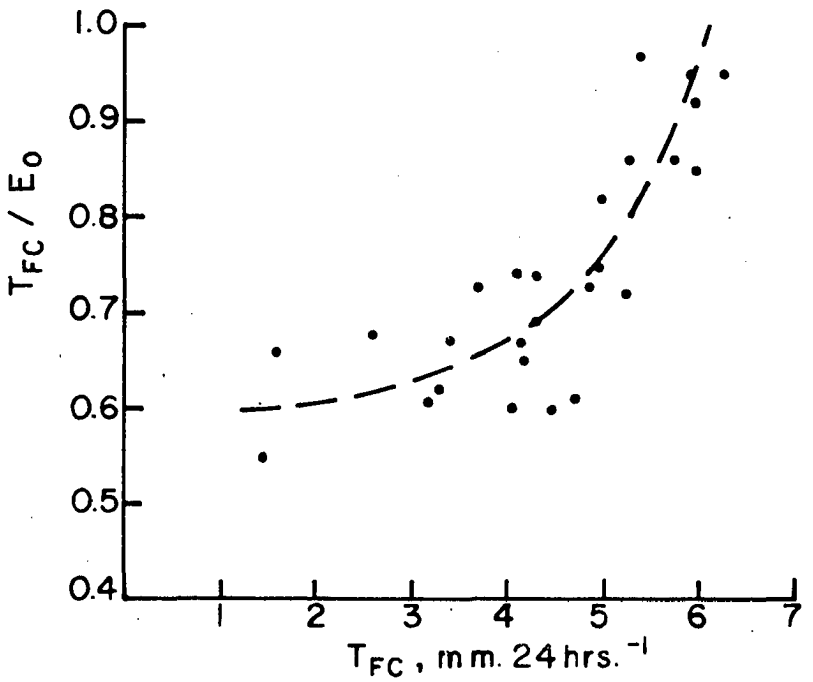


Figure 25. The ratio of the transpiration rate at field capacity T_{FC} to the estimated evaporation of an open water surface E_o, computed by the method of Penman (1956), as a function of T_{FC}

tential transpiration rate for crops of equal density would be about the same for all soils. As the soil dries, the influences of its moisture properties (suction and capillary conductivity characteristics) on soil water movement to the plant come into prominence, and differences between soil types in relation to relative transpiration rate become evident. But again, for any given soil type, the extent to which the soil properties affect the actual transpiration rate depends on the magnitude of the potential transpiration rate, itself a function of meteorological conditions. Thus, the availability of water for transpiration depends on the interaction between soil, plant and atmosphere, all of which must be considered in any discussion of this complex subject.

SUMMARY AND CONCLUSIONS

The dynamic aspects of the availability of soil water for transpiration have been considered in relation to the flow of water in the transpiration process. The water in the soil, the plant and the atmosphere form a continuum on an energy basis. Water moves through the soil to the plant roots and through the plant to the mesophyll cells of the leaf along energy gradients, moving from regions of higher potential (lower suction) to regions of lower potential (higher suction). At the leaf, water is evaporated into the atmosphere, the necessary energy for vaporization being supplied mainly by solar radiation. The evaporated water diffuses as vapor through the stomata and through a thin layer of saturated air adhering to the leaf surface into the free atmosphere where it is removed from the vicinity of the leaf by turbulence and convection and by diffusion along vapor pressure gradients.

By analogy with the flow of heat into an infinitely long cylinder, the mathematical solution of the equation describing the flow of water through the soil to the plant root in the transpiration stream can be obtained. In deriving the solution of the flow equation, certain assumptions as to root geometry and the constancy of both the capillary conductivity of the soil and the diffusivity for soil water flow must be made. Subject to these assumptions, the difference between

the soil suction at the root surface and the average soil suction in the root zone necessary to maintain a given rate of water uptake by the roots of the plant is a function of the capillary conductivity of the soil, the diffusivity for soil water flow, the rate of water uptake by the roots (itself directly proportional to the potential transpiration rate), the root radius, and time. The most important factors affecting this difference in suction are the capillary conductivity of the soil and the rate of water uptake by the roots.

Considerations of the solution of the flow equation show that the actual transpiration rate at any soil moisture content (or at any soil suction) depends on the moisture properties of the soil (suction and capillary conductivity characteristics), the maximum diffusion pressure deficit which can be developed in the plant tissues and the potential transpiration rate. Experiments with corn grown in large containers showed that the theoretical predictions concerning actual transpiration rate are qualitatively correct, although the experimental results indicated that turgor-induced changes in permeability of the plant to water movement may restrict transpiration much more than the theory predicts at high potential transpiration rates. The experiments showed that for moderate potential transpiration rates, the actual transpiration rate was very nearly equal to the potential

transpiration rate until the average soil suction had increased to a value of 1 bar. As soil suction increased beyond 1 bar, the actual transpiration rate declined rapidly. When potential transpiration rate was low, the actual transpiration rate did not decrease until the average soil suction had increased to a value of 5 bars. When potential transpiration rate was high, the actual transpiration rate decreased rapidly when the average soil suction exceeded only 0.2 bar.

In the experiments, it was found that when potential transpiration rate was low, some transpiration still occurred at an average soil suction of 40 bars.

The results of the experiments indicated that the maximum diffusion pressure deficit which can be developed in the corn plant is in the vicinity of 100 bars.

The dynamic theory of transpiration implies that there is a maximum to the transpiration rate from a plant, determined by the maximum diffusion pressure deficit which can be developed in the tissues of the plant. The experimental results indicated that such a maximum transpiration rate does exist and that its value for corn is in the vicinity of 6.6 mm. 24 hrs.$^{-1}$.

It is suggested that apparent discrepancies in the literature concerning the availability to plants of soil water within the "available" range can be reconciled by consideration of the various soil and weather factors involved.

If one assumes that plants wilt when the diffusion pressure deficit in the plant exceeds a certain critical value, it can be shown that the wilting point is governed by dynamic factors. The solution of the flow equation can be used to predict that the soil moisture content at which plants wilt, designated the turgor loss point, varies with the rate of water uptake by the roots, which is directly proportional to transpiration rate. Observations of transpiration rate in the field indicated that the turgor loss point varied considerably. When potential transpiration rate was low, the estimated turgor loss point approached the 15-bar percentage. As potential transpiration rate increased, the estimated turgor loss point also increased and approached a value close to field capacity. These observations were supported by visual observations of wilting in the field and by determination of plant growth rates. At low potential transpiration rates, the agreement between the theoretical and the observed turgor loss points was quite satisfactory, but at high potential transpiration rates, the observed turgor loss points appeared to be higher than the predicted values. It is believed that this discrepancy was due to a marked decrease in the permeability of the plant to water movement at the high transpiration rates.

The rate of production of dry matter of plants appeared to be related to the transpiration rate. When soil water was

readily available to plants, i.e., at soil moisture contents close to field capacity, their net assimilation rate appeared to be related to their transpiration rate. When the soil moisture content for control plants was maintained close to field capacity and the soil moisture content for other treated plants was allowed to decrease, the relative growth rate of the treated plants (their increase in dry weight/the increase in dry weight of the control plants over the same period) decreased at about the same rate as their relative transpiration rate (their transpiration rate/the transpiration rate of the control plants). In view of these findings, it is suggested that, under certain limiting conditions, viz., adequate soil fertility and a reasonably complete plant cover, the concept of the transpiration ratio may have some useful applications.

Grain yields were also found to decrease with decreasing soil moisture content. Grain yield appeared to be most severely reduced when soil moisture stress occurred at about the date of 50% silking.

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